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ANIMAL ECOLOGY

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BY

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TO

VICTOR E. SHELFORD

PREFACE TO THE SECOND EDITION

So much progress has been made in ecology since the first edition of this book was published that a complete revision has been necessary. It is believed that a more logical arrangement has been adopted. Seven new chapters have been added. The chapter on color in the old edition has been combined with that on animals. The two chapters on ecological factors have been amplified, but combined into one in which environmental influences are considered under the general headings of energy, media, and biological factors. New chapters include information on climate, evolution, chorology, succession, climaxes, rhythms, communities, competition, populations, teaching, ecological problems, and economic ecology. One hundred and thirty-two illustrations have been added.

Grateful acknowledgment is made to George W. Wharton, who read the manuscript of the first four chapters and proof of Chapters VII, XII, and XIII; to J. W. Littler, who prepared all the original drawings; and to the following colleagues who critically read proof: F. G. Hall, Chapters, I–VI, VIII, and XVI; I. E. Gray, Chapters, VII, IX, and XII–XV; and H. J. Oosting Chapters, V–VII, X, and XVII. Mrs. Hazel D. Rickman and Robert Wetmore gave valuable aid in the preparation of the manuscript and index.

A. S. PEARSE.

DURHAM, N. C.,
January, 1939.

PREFACE TO THE FIRST EDITION

One who writes a book that pretends to be a general survey of even a limited field of science is continually impressed with his own limitations. The writer is sure that there are many ecologists who could have done this work better. He claims no credit except that of doing the work, which is needed. This book is a very small beginning in a very large field, and future developments should make better books possible.

The writer is glad to express his appreciation to certain of his colleagues. Dr. L. E. Noland and Dr. E. S. Hathaway read and criticized the whole manuscript. Dr. E. J. Kraus made valuable suggestions in connection with Chapters I, II, and VII; Mr. Chancey Juday did the same for Chapters V and VI. Dr. A. F. Shull made many useful comments in editing the manuscript. These gentlemen have saved the writer from many errors but are, of course, not responsible for those that doubtless remain.

A. S. Pearse.

University of Wisconsin,
Madison, Wis.,
February, 1926.

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ANIMAL ECOLOGY

CHAPTER I

INTRODUCTION

Ecology.—Ecology is the branch of biological science that deals with relations of organisms and environments. It is concerned with responses of whole organisms, or groups of organisms, to environmental stimuli, and with changes in environments brought about by activities of organisms. It often makes use of physiological experiments to obtain knowledge and so tests the responses of parts of living organisms, but its generalizations deal primarily with the behavior of complete individuals or groups. Ecology is often divided into autecology and synecology, which deal respectively with relations of individuals or with those of plant and animal societies to environments. This book discusses relations between animals and environments. Plants and animals are so often and so intimately related in nature that it is impossible to consider one without the other; but modern science is specialized to such a degree that ecology is usually considered by botanists or zoologists rather than by biologists. It therefore seems expedient to present one side of the picture at a time.

Changefulness of Animals and Environments.—The study of ecology is difficult because both animals and environments change more or less continually. Every animal must maintain its metabolism or it dies. It digests, absorbs, assimilates, oxidizes, works, fights diseases, and excretes. The character of its metabolism varies with age, sex, and other conditions. Environments vary with seasonal and diurnal cycles, climatic changes, and other periodic and irregular fluctuations. Living organisms are unique in their ability to utilize energy so as to maintain their own complex systems of activities. The metabolic activities of animals in general are alternating continually between conditions in which systems are built up into rather stable states and those in which energy is discharged to do work

and in which systems often become more or less unstable. Thus rest and food must alternate with work and hunger. Energy and matter must be captured from environment, built into living substance, and destroyed in doing the work necessary to obtain more energy and matter from environment.

Brief Synopsis of Ecological History.—The first naturalist who made a serious attempt to systematize knowledge concerning relations of animals to environment was Buffon. In 1749 he began to produce a series of works in which he stressed habits and adaptations. Malthus (1803) published a treatise on populations which is still a classic. Humbolt (1807–) after extensive travels discussed the geographical distribution of plants and animals in relation to climate. Saint-Hilaire (1859) used the term "ethology" for the study of relations of organisms to environment and outlined a volume, which he never wrote, on instincts, habits, and other ecological matters. In 1869 Haeckel proposed "Oecologie" for the relations of organisms to organic and inorganic environments. Mobius (1877) introduced "Biocognose" to designate a group of organisms as an ecological unit. Wallace (1878–) in his essays on tropical nature, distribution, evolution, coloration, and other subjects presented stimulating ideas. Semper (1881) was a philosophical traveler who thoughtfully considered the conditions of existence under which animals live. Hensen (1887) made excellent quantitative studies of plankton. Forbes (1895–) pointed out that economic zoology is largely applied ecology. Schroter (1896) introduced the terms "autecology" and "synecology." Herdman (1896) indicated the economic possibilities of scientific aquiculture. Brooks (1899) in his "Foundations of Zoology" and other writings inspired thoughtful considerations of ecological problems. At the beginning of the twentieth century ecology was a young, but an established, science, and such eminent ecologists as Wasmann (1901), Dahl (1901), and Wheeler (1902) were discussing whether Saint-Hilaire's ethology or Haeckel's ecology should be used to designate the science of relations of organisms to environments. The latter term has gradually come into general usage. Case (1905) discussed environmental conditions of past geological periods and has continued to make contributions in that field. Two botanists, Clements, in his "Research Methods in Ecology" (1905) and subsequent writings, and Warming (English trans-

lations of "Oecology of Plants," 1909, 1925) have done much to clarify ideas and contribute terms. Adams (1913) gave an excellent review of significant ecological literature, urged the usefulness of ecological surveys, and discussed methods to be used in making them. Shelford (1912) demonstrated excellent examples of ecological succession and has made notable contributions concerning animal communities (1913) and environmental factors (1929). Huntington (1922–) has written several books that contain stimulating discussions of ecology in relation to human geography. Borradaile (1923) wrote a descriptive animal ecology. Hesse (1913) and Dahl (1921) have contributed works on ecology in relation to zoogeography. Elton (1927) in his "Animal Ecology" considered food chains and fluctuations in populations. Chapman (1931) also wrote a good work, with the same title, in which he stressed insects and the quantitative aspects of ecology. He also used the terms "biotic potential" to indicate the ability that organisms have to multiply and occupy an environment, and "environmental resistance" to include the factors that prevent organisms from realizing their full potentialities for increasing.

CHAPTER II

ENVIRONMENTS

Environment.—An environment is a complex of physical and biotic conditions which surrounds an animal or plant or a group of such organisms. From the broadest point of view it includes the whole universe, but for practical purposes the term environment is usually taken to mean the immediate surroundings of organisms (as a brook, lake, prairie, forest, host for a parasite), such as play significant roles in furnishing necessities of life and thus permit organisms to complete their life cycles and leave progeny. It is possible that organisms may exist on planets and heavenly bodies other than the earth, but, if they do, they must be adapted to quite different conditions. The knowledge that men have accumulated concerning ecology relates largely to the conditions on the earth—in fact, to those in a rather thin layer on the outside of the earth. The sun of course exerts a profound influence on earth environments and furnishes most of the energy that activates plants and animals. Its varying relations to different parts of the earth's surface and its periodic variations are the chief factors in producing climatic and seasonal changes. With the moon it causes tides and ocean currents. Other lesser or more remote bodies also exert some influence on conditions under which plants and animals live. Before taking up ecology in detail it is appropriate to consider the history of the earth and its characteristics as an environment for organisms. This discussion will necessarily involve climates and habitats.

Periodic Variations in Environments of the Earth.—The rotation of the earth on its axis produces diurnal changes. On the side away from the sun it is night; whereas on the illuminated side it is, of course, day. Conditions thus change every twenty-four hours—not only radiant energy, but humidity, gases, and other phenomena that may influence the lives of animals. As the earth each year traverses its elliptical orbit around the sun, seasonal changes occur. These are due primarily to the fact that the axis that passes through the poles of the earth is inclined

23.5° to the ecliptic, or the plane in which the earth rotates about the sun. When a pole is inclined away from the sun, the hemisphere in which it lies receives less energy and experiences winter; when the earth is on the other side of its orbit, summer comes in that hemisphere. At the equinoxes, days and nights are equal everywhere on the earth (Fig. 1). The moon rotates about the sun about every 29.5 days. It influences the earth chiefly by causing tides in larger bodies of water. Jupiter is the largest planet, and its enormous mass is great enough to produce changes in the sun that are significant on the earth. The period of rotation of Jupiter about the sun is 11.86 years. Saturn,

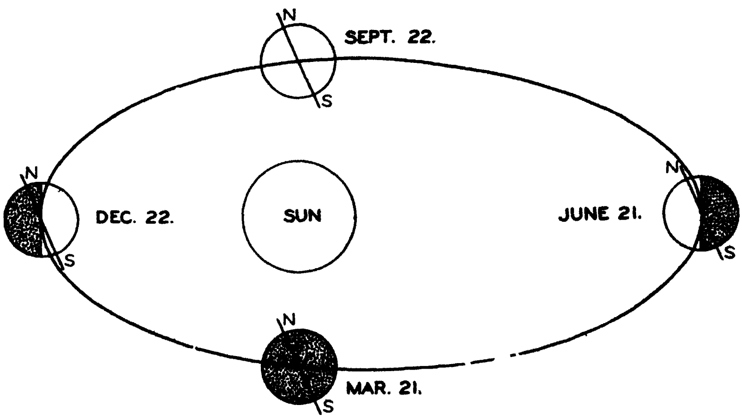


Fig. 1.—Earth's position in its orbit at spring and autumn equinox and summer and winter solstice; to show the inclination of the earth's axis to the ecliptic.

Mercury, and other planets also produce lesser effects. When planets of considerable mass in their orbital progression are close to the sun there are more disturbances on the sun's surface. These when viewed from the earth appear as sun spots. When there are many sun spots more energy is given off from the sun, but, as there are then more storms on the earth, less energy actually reaches its surface. The periodic variation in energy from the sun is known as the "sun spot cycle," which has a period of about 11.3 years. By studying the growth rings in the trunks of redwoods and other trees in the western United States Douglass (1919, 1928) has found evidence of 11.3 year cycles for 600 years, but trees in certain areas also indicated climatic cycles of 7, 14, and 21 years. Some observers believe that there are

longer cycles of 33–34 years (Brückner's Cycles), when variations in solar energy are more pronounced. At much longer intervals there have been glacial epochs, warm periods, arid periods, moist periods, etc. These have probably been due at least in part to variations in solar energy, ratio between land and water, elevation of land surfaces, electromagnetic activity, and perhaps other causes. Most of the past and present changes in climatic conditions on the earth appear to have been brought about largely by forces from without rather than from within the earth.



FIG. 2.—Growth curves for pines at Flagstaff, Ariz., as determined by growth rings. Cycles of about 11.3 years are shown for 600 years. (*After Douglass* 1928.)

History of the Earth.—Whether the earth began as a nebula which condensed or as a small solid body which grew by the accretion of planetesimals, and whether it was hot or cold when young, there seems to be general agreement among geologists that, since fossils began to accumulate, the crust of the earth has been solid and not very different from what it is today (Chamberlin, Reid, Hayford & Schlesinger 1917). The earth has also probably long been about the same distance from the sun. For several hundred million years, temperatures have not varied through a range of more than 60°C.—probably much less (Huntington & Visher 1922). It is remarkable that conditions have been so uniform for such a long time that life has persisted from Pre-cambrian times to the present. There have been glacial periods, when extensive ice sheets existed even in the tropics,

but the whole earth has never been so cold that life could not persist. There have been periods when mild monotony was widespread, and these alternated with periods of complex diversity. The chief factors that change, and have changed, the form of the earth are diastrophism, vulcanism, and gradation. Probably oceans have gradually grown deeper, and land masses higher. Again and again highlands have been uplifted and slowly reduced to base levels. Volcanoes have belched forth ashes, rocks, gases, and streams of lava. But it is probable that such changes have on the whole had less effect on earth environments than influences coming to the earth from outside. For example, Huntington and Visher (1922) postulate conditions that brought about and ended glaciation during the Pleistocene Period according to their Solar-cyclonic Hypothesis: Many sunspots prevailed while continents were elevated; carbon dioxide and plant growth decreased; there was little water vapor in the atmosphere. As solar disturbances continued, storm tracks on the earth moved toward the poles; precipitation increased, and ice sheets formed; storms raged along the margins of the ice; plants and animals of warm and cool regions mingled in milder areas. Then solar activity decreased; ice disappeared; storm tracks moved toward the equator; clear skies and aridity caused evaporation of ice and the water resulting from it. Doubtless many factors contributed to the coming and passing of glacial epochs. Among these have been suggested (Reeds 1921) the formation of mountains and ocean basins, volcanic activity, changes in the earth's orbit, decrease of solar radiation by passage of solar system through regions where there were no stars, lesser inclinations of ecliptic, decreased carbon dioxide, and rearrangements of areas of lands and seas.

Character of the Earth.—The earth has long been largely solid. At present it consists of a crystalline shell which surrounds a series of vitreous shells. The center is much denser (11) than the outside (2.77), and the average density is about 5.55. The earth acts as a magnet, but most of the exterior is nonmagnetic. Probably the center is nickel or nickel-iron alloy. The Theory of Isostasy, that the lightest minerals in general have highest elevations, is supported by known facts. Rock-forming minerals are comparatively few—mostly silicates of aluminum, iron, magnesium, calcium, sodium, and potassium. Twelve elements

(O, Si, Al, Fe, Ca, Na, K, Mg, Ti, H, P, and Mn) make up 99.61 per cent of the earth's crust (Washington 1922). Temperature increases with depth at the rate of about 1.0°C. per 36 m., or 28°C. per kilometer. Estimates by geophysicists give 760°C. at a depth of 30 km. and 1330°C. at 60 km.; some believe that the earth cannot be solid below 80 km., or 50 miles (Daly 1933). Liquids are at or near the surface. About the solid and liquid earth is the atmosphere, which consists of nitrogen 78 per cent by volume, oxygen 21 per cent, argon 0.94 per cent, carbon dioxide 0.03 per cent, and several rarer gases (helium, neon, ozone, hydrogen, etc.) 0.03 per cent. The atmosphere is probably 400 km. (250 miles) thick, perhaps two or three times as thick as that. It penetrates into pores and crevices in the earth and is absorbed in water. Particles of dust, vapor, and clouds may be carried in it. Plants and animals are of course confined to a narrow stratum at and near the surface of the earth.

Sources of Earth's Energy.—"The energy supplied to man in the past has been obtained wholly from the sun, and a billion years hence he will still, I think, be supplying all his needs for light, and warmth, and power entirely from the sun" (Millikan 1928). The physicist just quoted believes that atoms are continually destroyed in the hot interiors of stars and that they are rebuilt from electrons in cold interstellar space, chiefly into such widespread types of material substances as helium, oxygen, silicon, and iron. The energy that living things derive from processes taking place within the earth itself is negligible. As organisms need energy to activate their systems, they might be expected to flourish on the tops of mountains where they would be closest to incoming cosmic rays and solar radiation. But what is known of the evolution of plants and animals indicates that their origin was in the ocean and that through millions of years they gradually spread into fresh-water and land habitats (Pearse 1936, Baldwin 1937). Green plants require light for the manufacture of their foods; plants without chlorophyll and animals get their body-building materials secondhand from the foods stored by green plants. At present there is more, and in most respects better, food on land where most energy is available. The evolution of organisms in relation to energy will be discussed in Chapter V. On the whole it is generally true that the most progressive and modern types of plants and animals occupy land

habitats and the more primitive have remained in the ocean. Land habitats offer more energy but are subject to extreme variation in temperature, available water, and other environmental factors, whereas the ocean is stable and dependable and surrounds its inhabitants with a medium containing all the materials necessary for the manufacture of living substance.

Land Climates.—Meteorology is the study of atmospheric conditions in relation to climate and weather. It is concerned chiefly with temperature, barometric pressure, wind, and precipitation. Temperatures vary daily with the rotation of the earth on its axis and annually with the orbital progression of the

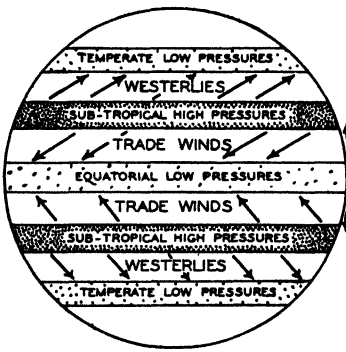


FIG. 3.

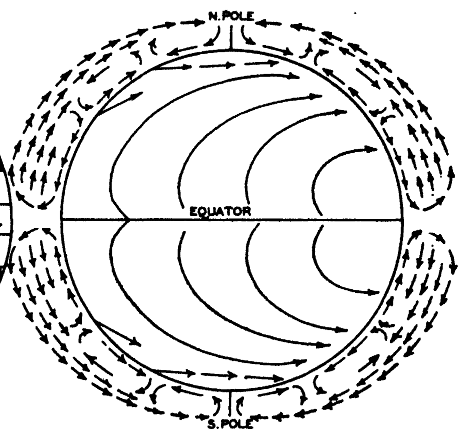


FIG. 4.

FIGS. 3, 4.—Prevailing pressure and wind systems of the earth. (*After Kendrew* 1930.)

earth about the sun. Large bodies of water tend to stabilize climates because water warms and cools slowly. Michigan lies between two great lakes and therefore has a more equable climate than North Dakota. Land areas tend to be colder in winter and warmer in summer than water areas. The earth may be divided into zones from equator to poles according to isotherms, or lines of equal means; maximum or minimum temperatures; or annual ranges of temperatures. When the atmosphere is warmed over an area its pressure decreases and it tends to rise; when it is cooled it becomes denser and tends to sink to lower levels. Thus regions of high and low barometric pressure, the "highs" and "lows" of meteorologists, are centers for atmospheric disturbance, and characteristic winds are associated with them. Winds do

not usually blow directly toward the center of a low but in the Northern Hemisphere rotate counterclockwise; and from the center of a high, clockwise. On account of daily and annual movements of the earth there are prevailing winds which are characteristic of various latitudes (Figs. 3, 4). These vary somewhat at different seasons. When the atmosphere is carrying water vapor and is cooled so that it is supersaturated, the water may condense as fog, dew, rain, snow, or hail. Regions of heaviest rainfall are in the tropics (Fig. 5). Various factors influence the amount of precipitation. A strong moisture-laden wind blowing against high mountains produces heavy rains, as on the

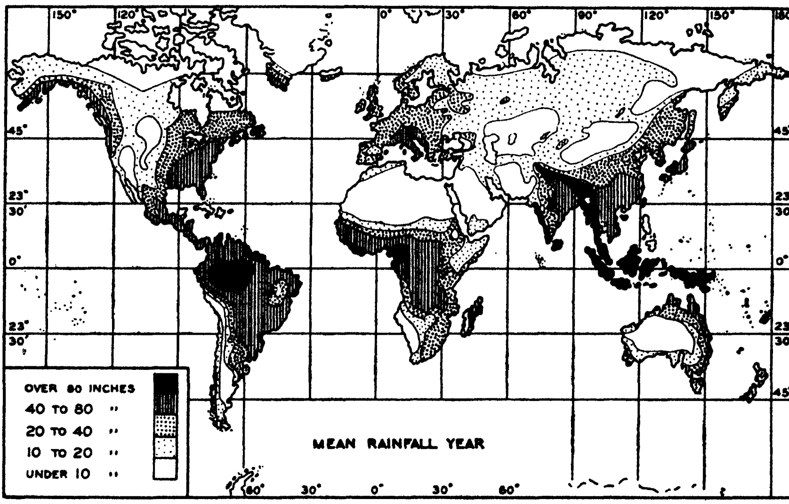


FIG. 5.—Rainfall on various parts of the earth. (*After Kendrew* 1930.)

east of the Andes and when the monsoons blow against the Himalayas from the south. South America has a heavy rainfall on the east but is arid west of the Andes; Africa is arid toward the north and east where it abuts on Asia but has a heavy rainfall on the west about the mouths of the Congo and Niger rivers. From the point of view of crop production or grazing, the season at which rain falls may be more significant than total annual precipitation. In temperate zones, rains at the beginning of the growing season are most conducive to the production of luxuriant plant growth and an abundance of animal life.

Ocean Climates.—Conditions in the hydrosphere are more stable than in the atmosphere. Though the sun shines on the

sea, the specific heat of water is so great that, with the cooling effects of evaporation and the ready mixing by convection currents, heating takes place much more slowly than on land. Currents in water are, however, slower and generally more constant than those in air. The ocean contains a rather uniform mixture of salts, but the amount of this mixture varies with place and depth, chiefly with the amount of fresh water entering as rain, snow, or inflow from streams and with loss by evaporation. Light penetrates only to limited depths. In the open ocean, currents are important climatic factors. They may bring about differences in temperature, salinity, transparency, and other features which are significant in the lives of marine plants and animals. Huntsman (1920) recognizes four grades of salinity in the North Atlantic (oceanic, bank, coastal, and estuarine) and three grades of temperatures (warm, intermediate, and cold); by combining these he defines 12 types of climate.

Fitness of Environment.—Henderson (1913, 1914) has discussed in an inspiring way the origin and properties of environments on the surface of the earth. He says in part (1914):

The properties of matter are not evenly distributed among the elements, nor in such a manner as can be explained by the laws of chance, nor are they altogether distributed in the manner which the periodic system describes. If the extremes be considered, all physical and chemical properties are distributed with the very greatest unevenness, so that the extremes are concentrated upon a few elements, notably hydrogen, oxygen and carbon. [Lillie (1913) points out that nitrogen might also have been mentioned] . . . The characteristics which make up this unique ensemble include the greater number of characteristics and especially the most important and the most conspicuous, physical and chemical properties. This order has for cosmic and organic evolution extremely important results—maximal stability of physico-chemical conditions and maximal complexity in the physico-chemical make-up of the surface of a planet; further the possibility of maximal complexity, durability and activity of physico-chemical systems in such an environment.

In fundamental characteristics, *viz.*, in the physical and chemical properties of water and carbonic acid and in other respects, the actual environment is the fittest possible abode of life. . . . It has been shown that the number of possible components (chemical compounds) consisting of carbon, hydrogen and oxygen is far greater than in the case of other elements; that the meteorological cycle mobilizes on land and sea

far greater numbers of other elements than would be the case if water were not the active agent in the process; that an aqueous solution is capable of holding a far greater number of components, in far greater concentrations than can any other; that water makes possible through its unique thermal properties and its unique qualifications in relation to colloids, the greatest possible number and variety of phases.

An activity is possible provided a suitable system exists and provided suitable energy is present. This fact leads us back to the conclusion that chemical transformations of hydrogen, oxygen and nitrogen are the very best means for storing and liberating energy, and that the reactions of organic compounds permit the most delicate adjustments of such transformations. Further it has been shown that the unique thermal properties of water are most highly suited to the storing of energy, while its solvent power facilitates osmotic pressure and diffusion. Finally it may be mentioned as a final instance of fitness for activity, among many other examples, that the electro-chemical characteristics of water are the best possible sources of electrical activity.

A very large part of the data of oceanography and meteorology do but illustrate the almost inconceivable efficiency with which water, in the main through its unique thermal properties, completely checks very wide ranges of temperature, and as a rule restricts the range of temperature within the waters and throughout the earth. Even more exact is the regulation of the alkalinity of the ocean by carbonic acid, through its unique solubility and ionizing power. These are but two among many examples of maximal efficiency in regulation.

The unique ensemble of properties of water, carbonic acid and the three elements constitutes among the properties of matter the fittest ensemble of characteristics of durable mechanism. No other environment, that is to say no environment other than the surface of a planet upon which water and carbonic acid are the primary constituents, could so highly favor the widest range of durability and activity in the widest range of material systems—in systems varying with respect to phases, to components, and to concentrations. This environment is indeed the *fittest*.

The special characteristics of the inorganic are the fittest for those general characteristics of the organic which the general characteristics of the inorganic impose on the organic. This is one side of reciprocal fitness. The other side may be similarly stated: Through adaptation the special characteristics of the organic come to fit the special characteristics of a particular environment, to fit, not any planet, but a little corner of the earth.

Basis for Classification of Habitats.—If life as it exists on the surface of the earth is dependent primarily on oxygen, carbon, and hydrogen, particularly as water and carbon dioxide, then

plants and animals will have relations first with water, which as an external medium brings various foods and removes wastes and as a body fluid forms the very basis of vital processes. The larger the body of water the greater will its stability be in regard to temperature and solutes. The oceans of the earth contain all the materials essential for life. Energy which activates vital processes comes largely from the sun. Radiant energy is absorbed rapidly as it passes through water, and deeper strata in the ocean must therefore derive their energy largely from the surface. On land, plants and animals are continually in danger of death from loss of water; temperatures vary greatly because the stabilizing influence of water is absent. Fresh waters vary greatly in gaseous content, salinity, and temperature. Quiet lakes and ponds are often stagnant below a shallow surface stratum. They offer quite different conditions for the maintenance of life from flowing, turbulent streams. On land there is often lack of water. In the scheme of classification of habitats presented at the end of Chapter VII it has seemed logical to begin with the most ancient and stable environment, the sea. It may be subdivided into three great regions: (1) the littoral, where radiant energy, tides, waves, and shores furnish a variety of homes for an abundance and wide assortment of organisms; (2) the pelagic, where light penetrates into the open sea; and the (3) abyssal, where animals live under great pressures in eternal quiet and dark. Next come the freshwater habitats: (1) swamps and pools, where water varies in amount at different seasons; (2) ponds and lakes, which are quiet, stratified, and often stagnant; and (3) streams, where water flows and silt often makes it turbid. Lastly come the land habitats, where various types of vegetation give characteristic physiognomy to each area. In these, water varies in amount; oxygen is abundant; temperatures vary greatly; and air, as a less dense medium than water, permits rapid locomotion.

CHAPTER III

ANIMALS

Animals.—An animal has been variously defined by scientific men as a system of activities, a dynamic agency acting in an unstable environment, a system in dynamic equilibrium, etc. "Organisms are not in equilibrium as long as life continues," . . . they "are not creative as regards either matter or energy, but merely directive" (Pike 1923). An animal consists of matter in the form of chemical compounds and conforms to physical laws but has an individuality which is peculiar in the type of its activities. It is ever changing yet maintains a certain average condition. The complex substances that make up the bodies of animals are built chiefly from those found in the atmosphere: carbon, oxygen, hydrogen, nitrogen; or, as they commonly occur in nature, as simple molecules or compounds: carbon dioxide, oxygen, water, nitrates, nitrites, and ammonia. Two views are held as to what constitutes an animal: (1) mechanists hold that an animal consists of matter energized by a peculiar and specific system of activities; (2) vitalists maintain that an animal consists of matter, energy, and also some vital principle that cannot be weighed or measured. Although neither point of view has been proved, most scientists, whatever their beliefs, proceed as mechanists in that they attempt to find scientific explanations for all phenomena associated with life. An animal, then, is to be defined as a highly complex system of activities which maintains itself under certain specific conditions in peculiar, highly complex bodies of matter. The activities result in self-maintenance, growth, repair, excretion, propagation, and other vital phenomena. An animal passes through stages of youth, maturity, and old age—the life cycle. Each animal has a peculiar constitution, or behavior pattern, which makes it unique among living things. Animals of the same species show more similarity than do those of different species, but each has an individuality. Behavior pattern limits the style of response that may take place in order to maintain an animal system of activities. A bass

does not pull earthworms out of lawns; nor does a robin hunt for insects among aquatic plants. One dog may bark and run from an intruder; another comes forward and bites. Each animal must meet environment on its own terms, or it is "like a fish out of water." Animals are adapted in a high degree to particular habitats, largely because they possess certain characteristics which are inherited from preexisting animals.

Plants Compared with Animals.—Plants are like animals in that their living substance appears to be much the same, but the representatives of each kingdom show certain specificities of response to the environment. Plants are generally sessile. They acquire from the earth and atmosphere inorganic materials which they make into organic substances. They respond in readily observable ways to various conditions in the environment by assuming particular forms of growth and, of course, may also undergo various internal changes which adapt them better to varying external conditions. Animals generally are motile, and stimuli often cause them to move; when they live in different habitats there is usually no pronounced change in form, but their bodies vary physiologically. Though there are many exceptions, it may be said that plants usually grow attached in one spot where they may acquire food from the soil, water, and atmosphere; where they can secure energy from the sun; and where they grow into a form adapted to the surroundings. Animals depend largely on organic food for their body-building substances and for more or less of their energy. Stimuli usually cause them to respond by movement, and they may thus migrate to places that are favorable for existence.

Adaptation.—An animal is said to be adapted when it fits the conditions found in some habitat on the earth. An individual fits because it has inherited certain qualities from its parents.

So far as we yet know every living species of plant and animal, including man, thrives best under limited conditions of temperature, humidity, and sunshine, and of the composition and movement of the atmosphere or water in which it lives. Any departure beyond the limits means lessened efficiency, and in the long run lower rate of reproduction and a tendency toward changes in specific characteristics. Any great departure means suffering or death for the individual and destruction for the species (Huntington & Visher 1922).

An animal is adapted because it comes into existence with certain ranges of toleration for various factors in its environment. A herring must live in water; a mudskipper (goby) can live on mud flats above water; a lungfish can live for months without water, encased in a dry mud cocoon; the larva of a dermestid beetle requires no free water at any time during its life and can live for several years without food. Every animal has optimum ranges of toleration for temperature, moisture, salinity, and other environmental factors. If conditions become supra- or suboptimum, life becomes more difficult. If they exceed the limits of toleration for an individual or a species, it ceases to exist. Where conditions are close to optimum an animal has a favorable habitat. Often one factor is close to the limit of toleration, and others are generally favorable. It then becomes for the time and place most important as a limiting factor. According to Leibig's Law of Minimum the factor in an environment that is closest to the limits of toleration or varies within a narrow range will be the limiting factor (Hooker 1917). "Considered from the most general point of view, it seems proper to regard adaptation as essentially an instance of equilibrium, though of a complex kind" (Lillie 1913).

Adjustment.—An animal that is adapted has certain powers of adjustment to changes that normally occur in its usual habitat, but such modifications of its system of activities will not go beyond its given specific and individual ranges of toleration. The limits of adjustment may differ among individuals of a single species on account of genetic differences or past experiences. A tadpole that has been reared at a low temperature dies more quickly and at lower temperatures when heated than one that has been reared at high temperatures. A jellyfish from the Gulf of Mexico will die when cooled to temperatures above 0°C., but an individual of the same species on the Labrador coast will remain active when surrounded by slush ice. Often young animals are more plastic and therefore able to make adjustments to rather extreme changes in environment which would be fatal to older individuals. In other instances young animals are delicate and quite unable to endure extreme environmental variations. There is little experimental evidence that adjustments to environment made during the life of an individual are transmitted as hereditary qualities. Such "acquired char-

acters" as palmar callouses and large arm muscles are not transmitted by a blacksmith to his son. A woman who has had smallpox does not bear immune children. Although every animal system of activities is free to make many minor adjustments, the main features and limitations that characterize it are set by heredity. This matter will be discussed again under evolution (Chapter V). It suffices to say here that adjustment is the aspect of adaptation that relates to ability to change an animal system to conform to a changed environmental system. Powers of adjustment enable animals to make internal changes, migrate to favorable environments, and endure unfavorable periods. In general, organisms have mechanisms that protect them from changes in environment; conditions within their bodies thus tend to remain uniform while environment varies. "As the complexity of organisms has increased, they have rendered themselves more independent of their external environment by providing their cells with an immediate environment of their own" (Wardlaw 1932). As a concrete example of adaptation and adjustment the coloration of animals will now be considered.

COLORATION OF ANIMALS

Color.—Color is a rather unsatisfactory word to use in connection with animals other than man, because colors are psychological products which are largely the result of human equipment for the sensory reception and interpretation of pulsatory movements of different rates of frequency which are known to science as light. An animal that responds to particular rates of vibration, or that discriminates between them, does not necessarily perceive colors as man perceives them. But though the quality of the sensations in man and other animals may be quite different, there is abundant evidence that certain animals are able to perceive what man calls colors and to respond to differences that are due to variations in the quality of light as distinguished from its intensity. When a surface reflects back practically all the light that reaches it, the effect as perceived by the human eye is white; when a surface absorbs essentially all the light that reaches it, the effect is black. Selective absorption may give various color effects.

Color Discrimination.—Wallace (1895) stated that animals have probably passed through a progressive series of changes—

at first possessing only a general sensitiveness to light, then developing more or less ability to discriminate between different wave lengths, and finally acquiring some power to discriminate and remember combinations of patterns. Many animals are unquestionably able to discriminate and form adaptive associations with what the human eye perceives as surfaces of different colors. Young barnacles attach themselves more readily to dark- than to light-colored objects; mosquitoes and bees are more likely to attack persons dressed in dark clothing than thos in light. The skins of flounders can closely simulate the backgrounds on which they rest in both pattern and color, and such simulation cannot be effected except by means of stimuli an received through the flounder's eyes (Sumner 1911, Mast 1916 There has been considerable argument as to whether certain animals possess color vision (Frisch 1923) or do not (Hess 192 g and much of the misunderstanding in this connection has been due to the fact that experimenters studied animals that w s adjusted to low or high light intensities (*i.e.*, were dark- or light adapted) and hence did not behave as they would if tested i intensities to which their eyes were at the time adjusted. Spa row (1923) has shown that the spectra of lights reflected fro animals do not correspond very closely with those of backgrour that the same animals appear to the human eye to match rath accurately in coloration and pattern. He suggests that colo may often be adapted for eyes that see in a different way fro those of man.

Colors of Animals.—From a physical point of view the colors of animals are due (1) to specific pigments that absorb certain light vibrations and reflect back others, (2) to structural peculiarities in surfaces that cause them to diffuse or refract rays of light. or (3) to combinations of absorptive, refractive, reflective, or diffractive influences. From the point of view of their usefulness in the lives of animals, colors, per se, may be classified as significant or non-significant (Poulton 1890). Many of the interna organs of animals which are never seen by friends or foes have characteristic colors which are probably of no adaptive importance but are to be looked upon as chance by-products of structure or physiological activity. Perhaps all colors were originally of this type, but some have become adapted so that they enter into relations that the animal bearing them has with its environ-

ment. The colors of animals in particular regions often have a general similarity. The crustaceans in the depths of the ocean are generally red; those in caves are often pale and pellucid; those in shallow, well-illuminated waters are decked out in various hues which more or less match the backgrounds on which they are usually seen. The colors of crustaceans in all three situations doubtless result from metabolism and other physiological processes, but the last type seems to be adaptive to a greater degree than the first two. It is undoubtedly true that differences in climate, as represented by variations in light, water, temperature, and other factors, influence the coloration of animals; also that different types of foods may lead to characteristic colorations. However, the fact that coloration is more or less a by-product, and not in all cases of adaptive value in relations with the environment, does not imply that certain colors may not be of relative or of prime importance in the adjustments of certain animals.

Adaptiveness of Colors of Animals.—Various views have been and are held in regard to the adaptive value of colors in animals and in regard to the types of uses that they may serve. There are those who hold that colors of all animals are merely results of metabolic activity and have little or no relation as colors to environment; others maintain that all significant colors are concealing (Thayer 1909, Longley 1917); and others that colors in animals may serve a variety of useful purposes (Poulton 1890, Carpenter 1937, Hingston 1935). One must be cautious in assigning functions to external pigments: black is advantageous in hot climates for animals (beetles) that do not live in direct sunlight, as it permits ready radiation and cooling (Parker 1935); a white exterior not only enables arctic animals to blend with snowy surroundings but also helps conserve heat (Frank 1933). There has been controversy between those who are impressed by the fact that many animal colors apparently are not adapted to any useful purpose and may be inherited without apparent reference to environment in accordance with the chance mixing of gene characters (Shull 1936, 1937) and those who have observed the remarkable way in which the colors and patterns of many animals match the backgrounds on which they live or how colors may serve for recognition of warning (Carpenter 1937). Among those who accept the adaptiveness of animal

colors there is dispute as to whether all colors are concealing (Thayer 1909, Longley 1917) or also serve for recognition, warning, and perhaps other purposes (Poulton 1890, Hingston 1933, Carpenter 1920, 1937).

Classification of Animal Colors.—Poulton's (1890) classification of the "significant" colors of animals is as follows:

- I. Apatetic colors—resembling the environment or some part of it:
  - *A*. Cryptic colors—concealing resemblances:
    1. Procryptic colors—resemblances affording protection.
    2. Anticryptic colors—resemblances aiding aggression.
  - *B*. Pseudosematic colors—false warning and signaling colors:
    1. Pseudaposematic colors—protective mimicry.
    2. Pseudepisematic—aggressive mimicry and alluring coloration.
- II. Sematic colors—warning and signaling colors:
  1. Aposematic colors—warning colors.
  2. Episematic colors—recognition markings.
- III. Epigamic colors—displayed in courtship.

Epigamic in this scheme might have been considered the same as aposematic colors if they had not been believed to be concerned with a type of recognition that involved some degree of appreciation of beauty as distinguished from that of a mere mark of identity. All matters relating to the coloration and uses of colors in animals are not yet on a scientific basis. There is need of more critical observations on the behavior of animals in relation to colors.

Concealing Coloration.—The Thayers (1909) did much to clarify ideas in this field. They stressed the fact that sight is often the important sense in enabling animals to escape from enemies or to find prey, because light travels essentially in straight lines and gives accurate information as to direction and location. They have made it plain that bright colors are not necessarily conspicuous and that animals conspicuous in certain environments may not be so in others. A successful disguise may be effective only at certain very short periods of time and at other times be of little or no importance for concealment or may even be conspicuous. Concealing coloration makes animals match the backgrounds on which they are seen and enables them to escape discovery by other animals. For example, iridescence tends to obliterate animals when they are seen on water or in

foliage. A bright spot reflected from an elongated, iridescent, moving animal that is seen among leaves may appear to stand still. Streaked bodies and barred tails tend to deceive a watchful eye as to the general form of the body on which they appear, especially when the body is among vegetation. The white tops of nocturnal animals, when seen by animals on the surface of the ground, tend to make the bodies of the animals that possess them blend with the sky line. Animals are generally countershaded, and this neutralizes the illuminating effects of light falling upon their bodies from above. The most highly illuminated parts are darkest, and the parts of the body that are in shadow are lightest in color; thus animals blend more readily with the surroundings by appearing to lose their appearance as solid objects interposed between the eye of the observer and the background.

Colors of Coral-reef Fishes.—Longley (1916), through his excellent studies of the gaudy fishes that live among and near coral reefs, has given strong support to Thayer's views concerning the importance of concealment as a general explanation for the coloration of animals. After prolonged investigation, much of which was conducted by means of a diving hood among reefs beneath the surface of the ocean, he concluded that the colors of reef fishes were largely adapted for concealment. Green fishes were usually associated with vegetation; blue fishes were found above the bottom, swimming freely in the open water; gray, as a type of coloration, was three times as common among fishes that swam about considerably as among those that were confined largely to the coral heads; yellow and brown seldom extended over a large portion of a fish's body and were often associated with gray; red fishes were largely nocturnal; banded fishes usually moved about much. Gaudy fishes were not avoided by predaceous animals but appeared as often as constituents of the foods of predaceous species as those that appeared to the human eye to be somber in hue.

Effectiveness of Concealing Coloration.—There seems to be no doubt that many animals are so colored that they are not readily observed by their enemies or by the animals on which they prey (Isely 1938). Desert animals are commonly decked out in dull grays and browns, and plankton animals are generally transparent. After a careful study of certain snails (Purpura) along

the New England coast, Colton (1922) concluded that size and shape were influenced to a considerable degree by environment, that shell sculpture and coloration were hereditary, and that the relative proportion of any color variety that might occur in a particular locality was due to selection. On light bottoms there were more light-colored snails, and on dark bottoms there were more that had dark colors. Di Cesnola (1904) has demonstrated that coloration has real protective value for mantids. He experimented with green and brown individuals which were picketed by means of threads on green or dead grass. Brown mantids were commonly eaten by birds when left on green grass but usually escaped notice when on dead grass, and the opposite was true of green individuals. In phasmids, color changes are induced by stimulation through the insect's eyes (Priebatsch 1933) and depend on hormone changes in the blood (Atzler 1930). Gerould (1921) observed that grass-green caterpillars remained unnoticed on grass but that mutants of blue-green type were soon devoured by sparrows. Mottram (1914) advanced the view that male birds are often brighter colored than females because they are of less value to the race. They may be destroyed after they have exercised their fertilizing functions without endangering the survival of the young. Mottram believes that their loss through the attacks of predaceous enemies serves to a certain degree to protect the females, because enemies are thus kept more or less in a condition of satisfaction in regard to their food requirements. Schreiner (1897) points out that the male ostrich sits on the eggs at night, and the female usually covers them during the day, and says: "It is scarcely possible to conceive a more effective disguise than the sober brownish gray of the hen for day sitting, and the black of the cock for night." Birds of both sexes, when on the nest, rest the head, neck, and tail on the ground and are very difficult to see.

Many animals show a high degree of adaptation for concealment, not only in general coloration but in pattern, form, and behavior. Carpenter (1920) gives many such instances among African animals. There are insects that resemble leaves or sticks, mantids and spiders that are able to catch their prey through their resemblance to flowers, etc. A South American fish, both in appearance and in movement, resembles a drifting leaf (Eigenmann and Allen 1921). The resemblance to the fronds that

surround them of the animals that live among Sargassum has frequently excited the wonder of observers. Even the nest linings and downy coverings of nestlings of birds are adapted for concealment (Linsdale 1936). Such instances of general and special resemblance in form and color might be multiplied almost indefinitely.

How Animals Resemble Backgrounds.—Apparently, the resemblances that individual animals show to their surroundings have come about by various means. In some cases they appear to be due largely to the effects of food, light, and other factors on metabolic processes; in others they are concerned with com-

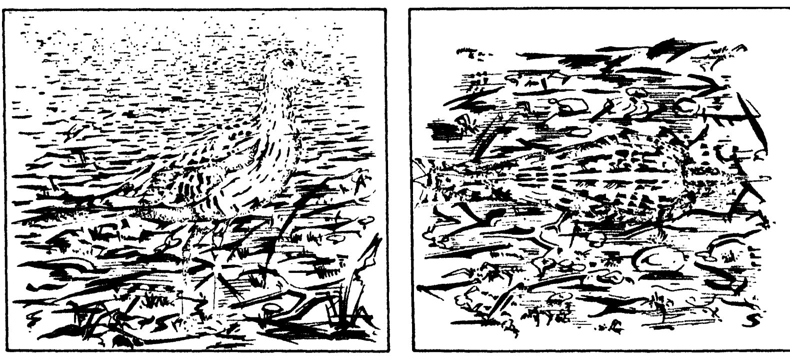


FIG. 6.—Perspective in the pattern of a shore bird as seen from the side and above and directly from above. (*After Thayer* 1909.)

plicated adjustments which involve nervous mechanisms. The Thayers (1909) have shown that background picturing without countershading is not effective in rendering animals inconspicuous. The color patterns that occur among animals are generally characteristic of well-lighted environments where there are a variety of color tones and patterns. Shore fishes and crustaceans wear varied coats; those in the deep sea are dressed in solid tones of black or red; those in caves are largely lacking in pigment. Burrowing dragonfly nymphs are monotone, but those that live on the bottom or among plants show varied patterns (Tillyard 1917). The background pictures on the bodies of many animals not only depict the backgrounds on which they are usually seen in great detail but also show perspective. For example, the markings on certain grouse and shore birds represent the lights and shadows that are characteristic of areas of vegetation; the

markings on the head and neck are smaller than those on the body, and thus to the eye of an observer the former blend more readily with backgrounds that are a little more distant than those against which the latter are seen (Fig. 6). Some animals picture backgrounds in a rather general way, and many are dependent on ruptive patterns, which do not represent average backgrounds in great detail but serve to break up the outline of an animal so that it is not readily recognized as being what it is. A butterfly that has black and white wings is generally less conspicuous than one that has wings that are wholly white or black. Thayer (1909) discusses many examples of such coloration.

Color Changes That Are Related to Environment.—There has been considerable discussion concerning the effects of variations in environmental factors on the coloration of animals in relation to backgrounds. There are a number of species of butterflies in which winter and summer, or wet- and dry-season, forms occur, and in a few instances these are believed to show variations that are correlated with patterns that are better adapted for concealment. Marshall and Poulton (1902) described "wet" and "dry" color phases of *Precis antiope* and affirm that "Adaptation . . . in the direction of conspicuousness, is characteristic of the under side of the wet phase." They believe that there is more danger from enemies during the dry season and that the butterfly is then better concealed. Poulton (1888) showed that the coloration of certain lepidopterous pupae was remarkably like that of the backgrounds around the larvae from which they came and that the color influence was potent when it affected a larva for only an hour before it transformed into the pupal state. Menzel (1913) has made similar observations. Clark (1921) has shown that a young shrimp, *Hippolyte varians*, is at first colorless but a week after taking up a sedentary life has come to resemble very closely the particular seaweed to which it is attached. Meinertzhagen (1921) states that crested larks are colored like the soils that they frequent and that they breed true to such colors, without reference to general humidity or rainfall. He says: "This same influence appears to affect nearly all ground birds which live more or less in the open." On the other hand, Sumner and Swarth (1924), who have made extensive studies of mice and other rodents, say: "Climatic factors, rather than the optical properties of the background, are responsible for the differ-

ences of color" and express the opinion that relative humidity is probably the most important factor in producing various coat colors.

Many animals are able to change their coloration and patterns to match different backgrounds. Some require considerable time to accomplish such changes, but others have them under nervous control and bring them about instantaneously. Tillyard (1917) states that dragonfly nymphs change colors more or less to match the environment. He believes that such changes are not brought about through the eye but are due to the "chemical plasticity" of pigment-forming substances just before or during molting. Such animals as tree frogs, chameleons, and lizards change their colors readily through the migration of pigment contained in cells in the skin. The migration may be effected by stimulating the pigment cells directly (with chemicals, light, or temperature), by indirect effects from stimuli received through the eyes, or by causes that apparently originate within the animal affected and are transmitted by the nervous system. Longley (1917, 1917*b*), Connoly (1925), Doflein (1910), and Sumner (1935) discuss the color changes of fishes and crabs. In general, they find that changes in shade may occur during short periods of time but that changes in pattern require longer. Mast (1916) has studied flounders which possess remarkable ability to change their colors and patterns to simulate backgrounds on which they rest and has shown that adjustment in pattern is dependent on stimuli received through the eyes.

Behavior in Relation to Background.—The behavior of many animals is such as to enable them to take advantage of their coloration by assuming relations that are favorable for concealment. Longley (1918) has shown that among fishes some types of coloration are suited for continual activity and others for sedentary life. In discussing birds Palmer (1909) says that habits of stillness are generally necessary adjuncts of protective coloration. The stone curlew has a crouching habit, which conceals it from enemies, when it hatches from the egg (Farren, 1907). Annandale (1902) describes a bright-colored beetle which frequents vegetation and is readily mistaken for a flower when quiet. It is active during the middle of the day, when its enemies are least active, and when disturbed at any time quickly drops to the ground and remains quiet. Longstaff (1906) and others have

noted that many butterflies alight facing away from the sun, so that they cast very little shadow, and, although Schrader (1909) maintains that they do this because they are thus able to see better, such a position doubtless aids in concealment. Longstaff (1906) gives many instances where butterflies when alighting selected the backgrounds that matched their own coloration. Mast (1916) states that flounders select backgrounds that match their own color and shade but do not show a high degree of discrimination in regard to patterns. Decorator crabs pick objects off the sea bottom and fasten these to recurved hooks on their dorsal surfaces. There seems to be no doubt that this instinct is adapted for concealment, but the crabs do not show color discrimination in the selection of materials for their decorations (Mast 1911, Pearse 1911).

Effectiveness of Concealing Coloration for Predator and Prey. In considering all cases of coloration it must be kept in mind that types of coloration and pattern that are effective for some enemies may not conceal from others. There are varying degrees of discriminative ability among predaceous animals that depend on sight for capturing their prey. Some animals are concealed as long as they are still and will remain immobile even when mutilated. Other animals that are well concealed when quiet disclose their presence by movement. Probably no means for concealment by coloration is universally effective against all enemies at all times, and such means do not enable predaceous animals that depend on concealing coloration always to secure prey. There is no doubt, however, that concealment is generally obtained by many animals through appropriate coloration (Sumner 1934, 1935, Isley 1938). Such coloration may, therefore, appropriately be termed "protective" or "aggressive."

Sematic Colors.—Warning coloration is characterized by conspicuous colors or markings that give notice to enemies of distasteful or injurious qualities. Recognition marks are conspicuous features such as those that enable members of a species to recognize each other or that facilitate the distinction of different types of individuals within a species. Many bright-colored and conspicuously marked animals that have been cited as furnishing examples of warning coloration or recognition marks will have to be reexamined in natural surroundings and in the presence of natural enemies before their validity as such examples can be

admitted. Longley (1916, 1917), studying communities of gaudily colored coral-reef fishes which had long been *assumed* to afford examples of warning or immunity coloration (Reighard 1908), showed that all the species he observed were colored primarily for concealment. He (1916) says:

> It is not demonstrated . . . that any class of markings serves for purposes of recognition, or for signaling between individuals of one species. Neither is it proved that some color combinations warn off possible enemies, nor, indeed, that any type of the pigmentation is functionally conspicuous.

Judd (1899) pointed out that many caterpillars that had been supposed to be warningly colored were not refused by birds on account of their coloration but because they were covered with hairs. He also called attention to the fact that rose chafers and aphids are seldom eaten by birds, although they are not warningly colored. For birds, color is only one of a number of qualities that may give notice of distasteful or harmful traits, and human standards for brightness of colors, distastefulness, or other qualities that make particular animals avoided may not be the same as those of birds that might molest them. Richardson (1914) has described a California lizard which commonly feeds on bright-colored flowers and warningly colored wasps. Marshall and Poulton (1902) state that spiders and mantids apparently have no appreciation of warning colors and that parasitic insects and robberflies commonly attack warningly colored insects. Warning colors may perhaps even be of advantage to parasites in finding hosts. Marshall and Poulton believe that all predaceous invertebrates probably have to taste each of their captures in order to determine its palatability. Folsom (1923) states that the use of recognition marks is not known among insects. Even the staunchest supporters of coloration for warning and recognition (Poulton 1890, Carpenter 1920) admit that it is not effective at all times and against all enemies.

Validity of Warning Coloration.—Notwithstanding the doubts that are raised when such evidence as has just been presented is considered, there appear to be many valid cases of warning coloration. The effectiveness of warning coloration in preventing attacks, of course, depends largely on the enemies concerned, particularly in regard to discriminative powers and ability to

remember and to form associations. Folsom (1923) believes that colors are of less value against insect aggressors than other qualities, such as odors and spines. Poulton (1890) long ago pointed out that the tastes of all insect eaters are not the same and also showed that frogs, lizards, and birds refused warningly colored insects, apparently through visual discrimination, after a little experience. Pocock (1911, 1911*a*) has called attention to the fact that shrews are protected from many predators by their rank and musky odor, that they squeak continually while running about and are, therefore, not readily mistaken for mice. In this case warning of distasteful qualities is given to enemies through sounds. Shrews are said to be killed and eaten by owls and are often killed by cats, which do not eat them. The Indian musk shrew is quite fearless, squeaks continually, and is conspicuous when running about at night. The same is true to some extent of the porcupine, hedgehog, and skunk. Among animals that have undesirable qualities, warning may be given by various means that are perhaps effective against certain enemies but not against others—conspicuous colors, odors, terrifying or startling sounds or appearances, etc.—or there may be no warning. Clark (1908) has noted that crinoids in their coloration show no apparent relation to environment, though warning coloration would be advantageous to them, for they are quite inedible. Certain animals that are apparently not offensive in any way may have bright colors, but this fact does not prove that warning colors may not be effective for certain animals that are offensive. The fact that many animals that have quite effective concealing coloration are also quite offensive does not prove that animals that are offensive and warningly colored do not profit by such a combination. Because certain animals that have adaptations for warning are eaten by certain enemies, warning through coloration is not necessarily a complete failure.

Discriminative Ability of Some Animals Is Adequate to Make Warning Coloration Effective.—There is apparently no doubt that fishes, amphibians, reptiles, birds, and mammals have a sufficient degree of *discriminative ability* to make warning *colors* effective (Frisch 1923). Perhaps certain arthropods may possess similar ability. It is not so clear, however, that all cases that have been cited as evidence of warning coloration have their basis in *color* discrimination, yet many of them appear to be

reasonably interpreted in such a way. It must be kept in mind always that objects distinguished by man solely on the basis of difference in color may be distinguished by another animal by some other sense than sight. Mottram (1918) and Jones (1932) give evidence that trout and birds avoid warningly colored insects because they possess distasteful qualities. Such cases as the following described by Carpenter (1903, p. 209) are difficult to interpret, except as indicating the effectiveness of warning coloration.

Just as cryptic insects must behave in accordance with the resemblance to their surroundings, so aposematic species have a behavior in keeping with their coloring. It would be of little use for a gaudy, distasteful insect to retreat timidly or endeavor to hide itself on approach of an enemy which, only partially seeing, might grab at it and damage it fatally before the mistake was found out. Everything is to be gained by flaunting the banner in the face of the enemy, so that there can be no possibility of a mistake. Consequently, aposematic insects are of the boldest demeanor, and are the species most frequently seen by the casual observer. If endeavors are made to catch one, for instance a *Planema* butterfly, it merely flits out of reach, and returns to the same spot unalarmed.

A large grasshopper, *Dictyophora laticincta*, family *Acrididae*, was frequently met with on the islands fully exposed on pathways: a bloated creature with heavy body, whose wings are so atrophied that it cannot possibly fly. So sluggish is it that it scarcely troubles to move out of the way, or gives a feeble hop merely carrying it for a distance about equal to the length of its own body. In color it is grey-black, and the short wings are scarlet, and there is some of the same color along the sides of the fat abdomen. If persistently annoyed it will raise the wing covers to show the red wings underneath. Such an insect, *a priori*, *must* be distasteful, and proved to be so when offered to my young monkey who would eat greedily until he was sick equally large, but procryptic, grasshoppers.

Many other apparently valid instances of warning coloration might be given. Poulton (1890) pointed out that warning colors that have developed in various groups of animals often show a tendency to follow the same general plans. This is, of course, advantageous; different species are thus of help to each other because fewer individuals are sacrificed in teaching predaceous animals that particular color patterns are associated with offen-

sive qualities. Such qualities are often localized on parts of the body where they may be readily presented to enemies—tussocks on caterpillars, nematocysts in the dorsal papillae of eolids, etc. In some cases conspicuous markings attract attention to a non-vital part, which may stand attack or even be lost without serious injury to the animal as a whole: "eye" spots on the wings of butterflies, antenna-like appendages on the posterior borders of wings, the tails of lizards, etc. Fowler (1918) has described a locust nymph in northern Africa, which is well concealed by its remarkable resemblance to the stones among which it commonly rests. When disturbed, however, it spreads itself out and takes on a form resembling that of a scorpion, at the same time displaying the bright yellow coloration on the inner sides of its femora.

Recognition Marks.—Morse (1907) asserts that bright-colored orthopterans are seen and followed by other members of the same species. He says:

> There can be no doubt in the mind of one who has watched these actions repeated over and over again that these colors are a means of signaling, of attracting attention, and thereby maintaining communication between sexes or individuals of a community.

Among orthopterans wing colors are commonly displayed during courtship. The writer (1914) has shown that male fiddler crabs wave their brightly colored claws when females are in view. Many birds display their colors, in some cases resorting to definite situations in order to dance and make such displays. Among many species the colors shown during courtship are concealed at other times. There appears to be little doubt that such exhibitions as are made by birds do serve to attract attention to particular sexes, but whether they are generally subjects of aesthetic appreciation among animals is questionable. Folsom (1923) states that the sexes of insects are often differently colored and that colorational antigeny is most often seen among butterflies, odonates, and beetles. He believes that sex differences in color have little or no protective value and that, though sex recognition on the basis of color among insects rests largely on assumption, it is plausible. Poulton (1890) asserts that recognition markings serve to keep gregarious birds together during flight. He cites the conspicuous white tails of the rabbit and

antelope as examples of recognition marks, but these are classified by Thayer (1916) as "flash" marks, which are believed to be concealing because they confuse a predator during the critical instant when it is attempting to grasp its prey. Poulton (1890) affirms that the markings on the eggs of colonial sea birds enable them to recognize their own eggs. Animals that develop bright colors during the breeding season are often particularly wary at that time.

Threatening Colors.—Hingston (1933) advocates the theory that certain animal colors and markings are for threatening or terrifying. On this basis he explains color displays, seasonal changes in color coats, and peculiar behavior when mating, capturing prey, or fighting. Often special markings are displayed when an animal is excited. A turkey cock spreads its feathers, gobbles, and erects the colored appendages on its head when it is threatening rivals, fighting enemies, or attempting to impress hens. Birds that show striking changes in plumage Hingston believes to show colors for different purposes at certain seasons. Mammals often display conspicuous callosities and color patches while they roar and behave in a threatening manner. Caterpillars and adult insects may assume peculiar attitudes, display bright colors and spines, and give off distasteful secretions when molested.

Mimicry.—Mimicry is the imitation in form, color, or behavior by a comparatively defenseless and edible species (mimic) of another species (model) that has qualities that cause it to be avoided by predatory enemies. The imitation is usually not conscious but is apparently brought about by natural selection among vibrations of hereditary patterns. The general idea of mimicry originated with Bates (1892), who stated that insects that had a bad odor or taste were commonly avoided by predators and that such distasteful species were mimicked in appearance by species that did not have bad odors or tastes. Müller (Longstaff 1912) introduced the idea that two species that are more or less distasteful may both derive benefit by resembling each other. Dixey has extended this idea into his theory of reciprocal mimicry or mimetic attraction. There has been much discussion concerning the origin and evolution of mimicry, and Longley (1917) gives a rather complete review of the work in this field. Wallace (1905) was the chief advocate of conspicuous (warning) color-

ation as a necessary accompaniment of mimicry. He laid down the following five conditions for Batesian mimicry:

(1) That imitative species occur in the same area and occupy the same station as the imitated. (2) That imitators are always the more defenseless. (3) That imitators are always less numerous in individuals. (4) That imitators differ from the bulk of their allies. (5) That imitation, however minute, is *external* and *visible* only, never extending to internal characters or to such as do not affect the external appearance.

Longley (1916) says:

> Mimicry has arisen through bionomic pressure applied first by indiscriminate feeders, which have forced upon their accustomed prey color combinations which most effectively conceal it in its normal environment. In addition, by chance, in a few of many thousands of cases in which colors appropriate to the surroundings and habits of their possessors have been evolved, patterns have appeared, sufficiently like one another to deceive enemies that exercise discrimination in the choice of food. From this point onward the evolution of resemblance has proceeded according to accepted formulae. without conspicuousness being involved in the process.

Longley believes that two animals become alike in coloration because they occupy the same habitats and have similar habits; *i.e.*, convergence in coloration follows convergence in habits and habitats. Punnett (1915) has advocated the view that mimicry has arisen through parallel mutations rather than by actual imitation (conscious or unconscious). Carpenter (1920, 1937) has presented excellent evidence that natural selection does operate to bring about mimicry.

Characteristics of Models and Mimics.—Models and mimics may be said to have certain general characteristics. The model must have offensive or undesirable qualities that make it avoided by predaceous enemies—chemical substances, spines, hard shell, habits of movement that make capture difficult, etc. There must be a tendency for animals to vary so that certain species or groups may come to resemble each other more or less. Finally, certain animals have apparently come to resemble others which serve as definite models. Semper (1881), Wallace (1905), and even Poulton (1890) to some extent, with other older naturalists, gave extensive lists of models and mimics without very definite knowledge of the habits or distribution areas of the species discussed.

There has been a more and more critical examination of the evidences for mimicry, and there are now a number of agnostics among competent naturalists. Eltringham (1910) states that conspicuous insects are often distasteful. Longstaff (1912) says that models need be only relatively impalatable; they may be eaten by certain species but not by others; they may be taken by extremely hungry animals; they need not necessarily deceive all enemies. Carpenter (1920) points out that a mimic's habits need not necessarily resemble those of a model closely. Farquharson (1922) in speaking of butterflies states that the flight of mimics is usually more rapid than that of models.

Examples of Mimicry.—There are many instances of mimicry that might be cited: hymenopterous models that are mimicked by flies, beetles by orthopterans, tiger beetles by crickets, wasps by crickets, etc. There are also examples of aggressive mimicry; for example, the resemblance of spiders to the ants with which they consort enables them to approach prey that does not avoid ants.

Criticisms of Theories of Mimicry.—Mimicry has not been accepted by scientists without considerable argument, and there are today many critics of current theories. Packard (1904) long ago argued that Müllerian mimicry had come about through the similar effects of light and moisture conditions on animals living in the same areas and expressed the view that mimicry as the copying of the coloration of one animal by another had not been demonstrated. Shull (1937) objects to current theories of mimicry because they do not consider the genetic origin of color variations. He claims that little or no knowledge of gene mutations is concerned. Thayer (1909) doubted that animals had come to resemble other animals, as such, but postulated the parallel development of color patterns to fit into similar environments. Wheeler (1922) mentions an instance among ants that belong to the genera *Gigantiops* and *Neoponera* that he apparently feels gives support to the same view. He says:

> Those who are interested in mimicry will observe that in its form, the dull black of its body and yellow antennal tips, Gigantopsis bears such a striking resemblance to *N. apicalis* and *obscuricornis* that the latter might be regarded as its models. Furthermore, these Ponerines sting very severely, whereas Gigantopsis can be picked up with impunity. In Kartabo, nevertheless, the models are much less frequently seen than the mimic.

Wheeler also points out that similar conditions have been found among butterflies and that among his ants the behavior of the so-called "models" is quite different from that of the mimics. Heikertinger (1933, 1934) thinks that the theory of mimicry has little support because the color patterns of butterflies are many and intergrade. Longley (1917), although accepting mimicry, does not believe that it is concerned with *warning* coloration as a characteristic of the model. He believes that coloration may be one of a number of qualities that may make an animal recognized as a distasteful one, but he does not believe that it is the factor primarily concerned in mimicry. He states that the coloration of animals that have geographic ranges that do not coincide at any point may be much alike. In parts of Japan there are beelike syrphids but no bees. Longley holds the view that not resemblances in color but those in habits and habitats initiate mimicry. Lutz (1911), Cockayne (1911), Punnett (1915), and Shull (1937) have doubts about mimicry because birds do not appear to eat butterflies to any extent and apparently do not exercise a great degree of discrimination in the selection of their food. McAtee (1936) has found that birds commonly eat insects that show warning colors. Manders (1911) has carried this argument further and claims that there are mimics and models among the butterflies of the islands Bourbon and Mauritius, where there are no insect-eating birds or other animals that could exert a selective action. He also claims that there is no butterfly-eating bird in Ceylon that can discriminate between different species of adult butterflies and that young birds learn to eat proper foods largely by imitating their parents. Punnett (1915) holds that the selective action of predaceous enemies is not important as a factor in producing mimics. He says: "The function of natural selection in respect of a mimetic likeness lies not in its formation but in its conservation. It does not bring about the likeness, neither does it accentuate it: it brings about the survival of those forms which happen to show the likeness." He affirms that there are no pierid mimics in Africa, though these butterflies are much persecuted by birds.

Support for Mimicry.—Among those who support the view that coloration is important in the development of mimicry, Swynnerton (1915) has done a great service by accumulating a large number of instances of attacks on and captures of butterflies by

birds. This observer states that inedibility is a relative term which depends upon the degree of hunger in an insectivorous bird but cites specific instances where mimetic resemblances have deceived birds. Longstaff (1912) observed that birds persistently tried to eat warningly colored insects but ate other insects first when they could be had. After experience, birds refused distasteful species. Marshall and Poulton (1902) fed insects to baboons and felt that they secured evidence of the effectiveness of mimicry. Eltringham (1910) affirms that conspicuous insects are usually distasteful. He found that lizards refused caterpillars that had been fed on ivy but ate those of the same species that had been fed apple leaves. Though this indicated discrimination on some other basis than coloration, he presents other evidence that indicates the operation of mimicry through coloration. Eltringham shows that both sexes of one species may mimic a female model of another and that females may mimic male models. Pocock (1911) carried on feeding experiments to test the effectiveness of mimetic resemblance. Poulton in an appendix to Pocock's paper says:

> With regard to the experiments on mimicry, it appears to me that they satisfied all that theory, as propounded by Bates, demands. They fully confirm Professor Lloyd Morgan's experiments on birds, with the dronefly (Eristalis) and the honey bee (*Apis mellifica*) as well as with banded and unicolored boxes holding respectively meal adulterated with quinine and meal untampered with. They show that several species of birds, after learning by experimental tasting that *Bombus hortorum* is unpalatable, refused to touch *Volucella bombylans*.

Pocock also showed that black beetles were unpalatable to certain ground-feeding mammals and that other distasteful beetles were commonly mimicked. Conspicuous lepidopters were commonly distasteful to birds. Though the tastes of birds and mammals were found to differ markedly, the species of insects that showed the greatest degree of cryptic coloration appeared to be most palatable. Bruel (1932) points out that mimicry is probably not of accidental origin because (1) it is largely restricted to day flyers, (2) mimics are usually changed only in characters that make them similar to their models, and (3) models are often poisonous, ill-tasting, or armed. Pseudomimicry (accidental similarity of nonrelated animals living apart) would refute mimicry only if it were more common than it is. Bruel argues that

protection for mimics does not have to be absolute; the deceptions would still be advantageous to the imitators.

Mimics That Behave As Their Models Do.—Perhaps the best support is given to colorative mimicry by the animals that not only look like their models but also behave like them. Pocock (1910) described the young of several species of mantids that resembled ants in appearance and movement, also young mantids that showed warning coloration and resembled distasteful bugs. Mann (1911), in Brazil " . . . observed the Proctutrypid, *Mimopria ectinophila*, with *Ection hamatum*, the host ant. The parasite runs along with the army of workers in an ant-like manner, and is sometimes picked up and carried by the ections."

Longley (1922) described a small fish on the reefs about Tortugas that picks parasites from large fishes, which apparently favor such attention, and it thus escapes attack. The small parasite picker is accompanied by a blenny which occurs in its schools in small numbers and resembles it in appearance and in movement.

Carpenter's Work.—Carpenter (1920) has given rather convincing demonstration of the effectiveness of colorative mimicry through his prolonged observations of African butterflies. He states that mimics are, in general, more easily alarmed and less resistant to injury than their models. He mentions certain spiders and capsid bugs which run about with ants and resemble them in appearance and behavior. He asserts his belief that certain warningly colored insects act as "centers" about which mimics are built up. Mimics may or may not belong to the same genus, family, order, or class as their models. He shows that, although bee eaters are especially fond of bees, these insects are commonly avoided by other species of birds and that their fly mimics profit accordingly. He points out that Longley's (1917*b*) explanation of mimicry by convergence does not satisfactorily explain resemblances in behavior between mimic and model.

Carpenter's (1920) best evidence for the dependence of mimicry on coloration is in his studies of the butterflies of the genus *Pseudacraea*, which commonly mimics several models. Many of the species of *Pseudacraea* (family *Nymphalinae*) are dimorphic. One species has 15 forms, certain of which mimic at least 8 species or subspecies of the genus Planema (family *Acraeinae*). Where selective agents and a single model were absent, various color

varieties of the mimic occurred together. Carpenter bred eggs from some varieties and obtained adults that belonged to other varieties, which usually did not occur where the parents lived. He found that localities where particular models were absent also lacked the mimic for that color pattern, though other varieties that had models present persisted. His observations and breeding experiments appear to demonstrate the effectiveness of mimicry and the validity of selection by predaceous enemies as a factor in eliminating certain color varieties and fostering others.

One of the remarkable points in the resemblances is the fidelity with which a single polymorphic species mimics sundry species of models of very different appearances in different localities; and where a model is sexually dimorphic the sexes of the mimic faithfully copy the corresponding sex of the model. Yet in the very locality where this dimorphism of model and mimic exists other species of monomorphic models are closely copied by monomorphic forms of the same species of mimic.

In some instances the models of one species were seen to be courted by the mimics of the opposite sex.

Adaptation and Coloration.—The coloration of animals has been considered as an example of adaptation. It is typical in that the adaptations cited are not perfect. Some colors are incidental or accidental products of genetic constitution and metabolic activity and have no apparent relation to colors in environment. Others may under some circumstances protect an animal on which they occur by concealing it or by warning enemies that it is undesirable; others may give notice of desirable qualities. Some color adaptations are remarkable for the high degree of fidelity with which they permit animals to fit into an environment and for the remarkable adjustments that enable them to match environmental tints and patterns.

Classification of Animals

For an ecologist, knowledge of animal classification is often necessary. When he goes afield to study habitats, he must be able to recognize species that are characteristic. They often serve as indicators of subtle changes in environmental conditions. Some varieties of species are physiologic, ecologic, and geographic forms—products of adjustments to environment; others represent differences in genetic constitution. The following list of

phyla of animals is taken from a more complete list of larger groups of animals published by the writer (1936).

Protozoa. Single cells; no somatic tissues.
Porifera. Tissues; no enteron; canals; include sponges.
Coelenterata. Radially symmetrical polyps and medusae.
Ctenophora. Comb jellyfishes with rows of paddle plates.
Platyhelmintha. Flatworms; planarians, trematodes, cestodes, etc.
Acanthocephala. Thorn-headed worms; intestinal parasites, without enteron.
Rotatoria. Small wormlike animals with ciliated trochal disks.
Gastrotricha. Small ciliated freshwater worms.
Echinodera. Small marine worms.
Nematomorpha. Horsehair worms.
Nematoda. Round worms with mouth and anus; many parasitic.
Tardigrada. Small aquatic animals with four pairs of appendages.
Chaetognatha. Arrowworms; marine.
Bryozoa. Colonial animals with tentacles; marine and freshwater.
Brachiopoda. Marine stalked animals with dorsal and ventral shell valves.
Pterobranchia. Wormlike marine animals.
Enteropneusta. Wormlike marine animals, with gill slits and proboscis.
Echinodermata. Radially symmetrical starfishes, echinoids, crinoids, etc.
Annelida. Metameric worms; marine, freshwater, land.
Gephyrea. Nonsegmented marine worms.
Onychophora. Wormlike terrestrial animals; paired appendages and nephridia, tracheae.
Arthropoda. Metameric animals with paired, jointed appendages and exoskeleton.
Mollusca. Nonmetameric animals with muscular foot and mantle.
Chordata. Chordate animals: ascidians, lancelets, fishes, amphibians, reptiles, birds, mammals.

CHAPTER IV

ECOLOGICAL FACTORS

Factors and Causes.—It is common practice among ecologists to say that an animal responds to a certain factor, such as humidity or temperature, when it shows a particular distribution in relation to conditions of environment or when it makes adjustments that tend to enable it to fit environment better. In attempting to discover why animals are so closely associated with particular habitats, one is continually led to look for causal factors in the environment. When an ecologist says that a certain factor is a cause, he, of course, understands that the word "cause" is used in a very general sense. A bass must live in water, and it is perhaps proper to say that water is the primary and most essential factor of the environment in which a bass lives. In one sense water is the primary cause of the existence of the bass system of activities, and the absence of water might be the cause of its extermination. But water is not the only cause to be found in bass environment, and it is perhaps no more essential than many other less apparent "causes." The environment must be complete, and one "factor" cannot make it so. When it is said that a particular factor is a cause, it is understood that this is merely a way of saying that the particular factor is the important, apparent, or immediate cause of any particular relation between an animal and its environment. Factors never act alone.

In their relations with animals, environmental factors may be divided into two groups: (1) physical and (2) biological. The first group is largely concerned with energy and chemical combinations in the inorganic environment; the second, with influences due to living organisms in the environment. In this chapter the chief physical factors are considered under the convenient headings: energy, as represented by light and heat; and media, such as atmosphere, water, and soil. Under biological factors are discussed extraorganismal relations: plants, animals, and fitness; and intraorganismal relations: structure, function, toleration, nutrition, growth, respiration, excretion, and behavior.

General geographic and ecological influences, such as edaphic and climatic factors, affect animals in essentially similar ways as do local factors. The causes of local habitat relations usually furnish the keys to the geographic distribution of a species. Each factor may be said to have a certain optimum condition for each living organism and has a certain range of variation, from maximum to minimum limits of toleration, throughout which a particular type of animal may be able to exist; but, from the point of view of an animal, an environment consists of more or less clearly defined units which are combinations of factors. If a single group of factors dominates a region, there are usually few species; but if there are many environmental units, or habitats, there is usually a considerable number of species. Where one group of dominant animals merges into another there may be zones of different types of animals throughout transition areas.

In the following discussions, where factors are considered separately, it must be constantly remembered that factors seldom act so, but influence animals as parts of complexes.

PHYSICAL FACTORS

Energy

Most of the driving force that activates animals comes directly or indirectly from the sun. Available radiant energy on different parts of the earth varies greatly. It also varies on particular areas at different times in annual and daily cycles. Solar radiation passes through the atmosphere quite readily, but water quickly absorbs ultraviolet and infrared radiations. At great depths in aquatic habitats all direct radiation is cut off, and animals exist in cold and dark. Animals originated in aquatic habitats and spread over land areas, where more radiant energy is available. In other words, the more specialized, modern types of animals have gradually invaded terrestrial habitats, where much energy is present but where certain factors vary within wide limits and where conditions of life are severe. In general more primitive insects live in comparatively stable habitats, and specialized animals are active in places and at times where and when most energy is available (Kennedy 1928). A hot, sunbaked field receives more energy than a cold, lightless cave; the tropics, more than boreal regions. Kennedy says:

The series of insects, from slow with low metabolism to fast with high metabolism, tend to be found in environments of parallel energy intensities. The slow insects (usually primitive) occur in environments of low energy intensity, in environments that are cool and shady or even dark; while the fast insects (usually modern types) occur in the light, hot environments of high energy intensity such as the tropics, the mid-summer, or the mid-day.

Early land vertebrates were small and swift, but many types which grew to be gigantic and slow became extinct (Osborn 1917).

Temperature

Range of Temperatures.—Theoretically the range of possible temperatures extends through about three billion degrees centigrade from "absolute zero" at −273°C. to high extremes far

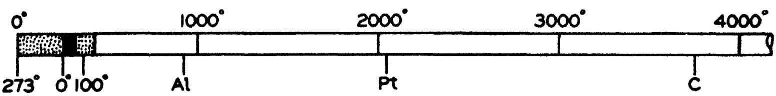


Fig. 7.—Comparison of absolute, or Kelvin's (K.), and centigrade (C.) temperature scales; with melting points of aluminum, platinum, and carbon. (*After Belehradek* 1935.)

above anything possible on the earth (Belehradek 1935). Of course animals and plants can exist in a very limited part of this great range, near its lower end (Fig. 7). Most species are active between 0.0 and 40.0°C., but some animals live all their lives below the freezing point of water, and a few regularly live above 50°C.

Nature of Heat.—Heat may be received or lost by animals as molecular vibrations transmitted from one part of an environment to another by radiation, convection, or conduction. It may be received as radiant energy, of course largely from the sun. It may be produced by mechanical work or by chemical reactions. A low temperature is called "cold," but everyone understands that heat and cold are relative terms and that a hot object differs from a cold object of the same sort only in its higher rate of molecular vibration.

Temperature and Climate.—Temperature is the chief criterion used in determining climate on different parts of the earth. Climatologists determine average temperatures for particular localities by averaging daily or monthly means. In temperate regions 40 to 60 years is required to obtain a reliable average; but

in the tropics, where climates are equable, only 2 years is required. At Quito, Ecuador, the mean annual range is 0.5°C.; at Batavia, Java, 1.1°C.; but at St. Paul, Minn., it is 33.7°C. In general, plants and animals are distributed across continents and vertically on mountain ranges according to temperature zones which are correlated with differences in latitude and altitude. Hopkins (1918) proposed a "Bioclimatic Law of Latitude, Longitude and Altitude." He pointed out that in spring, seasonal progression in eastern North America is later northward, eastward, and upward—generally 4 days later for each degree of latitude, 5 degrees of longitude, and 400 feet of altitude. The reverse is true in autumn. Various types of vertebrates are arranged more or less in zones from tropics to polar regions (Allen 1907). Cold air is usually dry air, and rays from the sun tend to turn water into vapor. When a tropical sun, a mountain range, and a cold ocean occur in the same region, as along the borders of Peru and Chile, the result is an extremely arid climate. When moisture-laden tropical winds are free to blow over a flat valley there is usually heavy rainfall, as in the Amazon basin Climate, as determined by temperature and moisture, is of prime importance in determining availability of terrestrial habitats on the earth. Areas where man has reached his highest cultural levels coincide rather closely with regions of optimum climate. When animals are transferred from one climate to another, the effect is more pronounced if they go from warm to cold than in the opposite direction (Gadow 1913). Tropical animals may live in cold climates but usually do not propagate. Insects that are introduced into cold climates tend to live longer. They often die when there is rapid alternation of cold and warm periods. On parts of the earth where there are marked seasonal cycles, temperature is one of the dominant factors in limiting the activities of many animals. The appearance and disappearance of certain migratory birds; continuance or cessation of parthogenetic or amphigenetic methods of reproduction in insects, crustaceans, rotifers, etc.; the spawning of molluscs and fishes; rapid multiplication of plankton organisms; and many other activities are more or less dependent on appropriate temperatures. Certain relicts in freshwater show their relations to their ancestors by breeding during the coldest season, when conditions are closest to those in the ocean (Ekman 1920).

Thermal Stability.—Most animals continually seek for stability in the environment. In the past, many types have left the water, which has a considerable degree of thermal stability, for the land, which offers gaseous stability. Absolutely stable temperatures are seldom attained in earth environments, but where they are approached, or actually obtain, animals usually flourish; where there are sudden, irregular variations, animals are often not able to live. Temperatures near the limits of toleration for animals may be withstood if they come about gradually. Survival of extremes is usually less dependent on the degree than the rate of change. On the other hand, the more rapid a thermal change is the more effective it usually is in stimulating animals. In the North Sea (Hesse 1913) there is an abundant fauna in regions where there is uniform, though extremely low, temperature; and a scanty fauna where the temperature varies. Huntington (1922) has shown that the human race is most productive where temperatures vary and accomplishes least in localities where there is a monotonous climate.

Temperature and Seasonal Variations.—Temperature is the most important causal factor for seasonal procession. In parts of the tropics where there is little seasonal variation in temperature, there is often a lack of periodicity in the reproductive activities of animals. The seasonal cycles on the earth are due largely to periodic variations and are accompanied by corresponding fluctuations in humidity, precipitation, dissolved gases (in water), and salinity (in the ocean).

Thermal Stratification.—The two common environmental media, water and air, when undisturbed tend to become thermally stratified, and such stratification is, of course, most pronounced in water—where it often leads to the establishing of seasonal or perennial zones of animal life. The deepwater fauna is a cold-water fauna, and many of its members do not range into regions where there are higher temperatures. Cases have been reported where organisms were found in a particular stratum of intermediate water and were few or absent in regions above and below, where temperatures were respectively higher and lower. In the Rocky Mountains, Dodds (1917) found that the microcrustaceans that had a limited range of toleration to temperature changes had a restricted vertical range. Michael (1918) says of the salpas:

Solitary forms show an increasing preference, so to speak, for the surface, as the temperature of the surface water increases from 16 to 20°C., while aggregate forms show a similar preference as temperature decreases.

The animals that live in the region between the tide marks on ocean beaches show a zonation that is in part due to the limitations set by temperature. On land there are also stratification effects that are due to temperature. It has been noted by many observers that the alpine faunas are related to those in the arctic and antarctic and that they do not invade the lowlands to any extent.

Temperature and Metabolism.—Temperature changes have a more or less direct effect on metabolism. Of course, an animal cannot survive supramaximal or subminimal temperatures, but the optimum rate of metabolism is usually much closer to the maximum than the minimum. This fact, together with observations on the metabolism of animals, justifies the assertion that, within certain limits, the higher the temperature the more rapid will be the rate of metabolism. Most animals live faster at higher and slower at lower temperatures. Stylonichia divides once a day at 7–10°C. and five times a day at 24–27°C. Esquimo girls that live in warm houses and have plenty of clothing reach maturity as early as girls in the tropics, but those that live an exposed life outdoors mature much later. Many animals, though not wholly inactive, cease to feed at low temperatures; others pass through periods of cold in a hibernating state during which the rate of metabolism is extremely low. Development may be prolonged on account of cold; annuals may be transformed, for a time, into biennials. The number of animals growing to maturity and their individual sizes may depend on temperature. Weymouth (1918) has cited instances where crabs, oysters, and salmon on the Pacific coast were larger after seasonal temperatures were high, early, and long, thus giving opportunity for early spawning and a longer growth period. Cyclic metabolic activities, like reproduction, are often influenced by temperature changes. The breeding periods of marine animals usually continue throughout favorable temperatures and generally begin (1) at the close of periods of minimum temperatures and (2) at the close of the maximum temperatures (Orton 1920). Cladocerans, rotifers, and aphids have different types of reproductive activity asso-

ciated with various temperatures, sex and sexual reproduction being controlled more or less by temperature variations. But the metabolism of some animals, on the other hand, is not essentially changed by temperature. Artemia eggs, for example, do not hatch sooner at high temperatures.

Temperature and Metabolic Rate.—According to van't Hoff's Law (= Rule of Q_{10}), the velocity of chemical processes increases two to three times with each rise of 10°C.:

$$Q_{10} = \left(\frac{K_1}{K_2}\right)^{\frac{10}{t_1 - t_2}} = 2 \text{ to } 3.$$

K_1 is the reaction velocity at temperature t_1. Metabolic process may conform to this law in a general way if temperatures are not close to or beyond the limits of toleration for an organism, but such conformation is not on the whole very exact. A living organism is a very complex system of activities. Organic reactions are often influenced by enzymes and other agents. The Rule of Q_{10} has been generally abandoned for Arrhenius' Law, in which μ is roughly synonymous with Q_{10}, and which appears to fit reactions that continuously take place in living things somewhat better, but also fails to fit observed metabolic phenomena. Arrhenius' Law expresses thermal increments as related to absolute temperatures. Robertson (1920) has compared the two types of expression (Table 1).

TABLE 1.—COMPARISON OF THERMAL INCREMENTS AS EXPRESSED IN Q_{10}(°C.) AND μ VALUES (calories required to transform 1 gram-equivalent of inactive into active molecules of a reacting substance)

Q_{10}	μ
2	13,200
10	44,000
100	88,000
1,000	132,000
10,000	176,000

Many persons hold that metabolic processes are controlled by "master reactions" which take control, so to speak, at "critical temperatures." A master reaction (Hoagland 1935) is the slowest reaction in a metabolic system; its rate limits all other reactions in the system. At critical temperatures an enzyme becomes effective, or a reaction takes place that markedly changes metabolic rate. Each dominant reaction has a different constant,

critical temperature. Crozier (1926) believes that these occur at 4.5, 9, 20, 25, and 30°C., but others (Powsner 1935) do not believe that such definite points are demonstrable. There is abundant evidence for the influence of temperature on metabolic processes. A fish consumes three times as much food at 20°C. as it does at 10°C. (Hathaway 1927); ants crawl progressively faster at higher temperatures; the rate of the rhythmical chirping of tree crickets grows steadily more rapid; in poikilotherms heartbeat, respiration rate, and oxygen consumption increase; fission in protozoans is more rapid; etc. Dorna (1932) proposes a physiological classification of climates based on heat loss in gram-calories per minute from the human body. He makes six classes: (1) 600, very hot; (2) 600 to 900, hot; (3) 900–1100, warm; (4) 1100–1300, cool; (5) 1300–1500, cold; and (6) over 1500, very cold. In an animal's body the optimum temperatures for activity may be unlike for different processes. In an oyster the cilia on the gills pump most water at 27–28°C., but the maximum relaxation of the muscle that opens the aperture between the valves occurs at 20°C.; so the muscle inhibits the greatest ciliary efficiency (Hopkins 1935), and the optimum temperature for the whole animal is 20°C. for pumping.

Thermoregulation.—The temperatures of animals that do not have some mechanism for maintaining their bodies in a constant thermal state do not differ much from surrounding media but are often a little higher (or lower), depending upon recent metabolic activity. As a whole, animals may be divided into two groups: (1) poikilotherms, or variable-temperature animals; and (2) homeotherms, or constant-temperature animals. The latter are well fitted to live in terrestrial habitats where temperatures and humidities may vary greatly. Only birds and mammals are homeothermic, though some other animals, such as ants and bees, make rather ineffective attempts to maintain their body temperatures at high enough levels for active metabolism during cold weather by gathering into groups, exercise, insulation, and migration to regions heated by solar radiation. Animals are all able to adjust their rates of metabolism more or less to temperatures higher or lower than those to which they have been previously acclimated. Such metabolism-regulating mechanisms operate slowly but are the basis for the more or less automatic changes which in homeotherms keep body temperatures constant.

A poikilotherm that is kept at a higher temperature than that to which it has been accustomed at first shows a more rapid metabolic rate but gradually slows down to about the level that it had before. In general, the opposite condition obtains when a poikilotherm is kept in a slightly cooler environment; at first its metabolism slows and then gradually rises somewhat toward the previous rate. A mammal maintains its body temperature near 38°C.; a bird, at about 42°C. During the first nine days of its life a young passerine bird is poikilothermic; its respiratory rate varies with temperature changes, and it consumes less food than it does later (Baldwin 1932). During cool weather many insects orient themselves to the sun in such a way as to obtain maximum radiation; during hot weather insects commonly orient themselves to the sun so as to expose least surface to radiation, raise their bodies above the soil, and crawl up on vegetation to escape radiation from soil. Regulation of body temperature by evaporation does not occur commonly in insects (Bodenheimer 1934), but evaporation of water keeps colonies of bees and wasps from overheating. Poikilothermal animals must live as the surrounding temperature dictates, and perhaps on this account many have often become adjusted to cold and stability rather than to a higher average temperature that fluctuates.

Stenothermic and Eurythermic Animals.—Animals are often classified into two groups: stenothermic and eurythermic, the former being restricted to a narrow range of temperature changes, and the latter having ability to live through a wide range. The optima for different species of animals vary greatly, and representatives of a widely distributed species may show different optima in various parts of the territory in which they are found. The eggs of many fishes develop best at temperatures that are little above the freezing point of water; the optimum for birds' eggs is close to 40°C. Amphipods swarm in the polar oceans, and dragonfly nymphs live in water that is considerably warmer than the human body. The medusa, *Aurellia aurita*, at Tortugas is killed if subjected to freezing temperatures, but individuals at Nova Scotia readily survive such treatment (Mayer 1912). The optima of comparable animals living in the frigid and torrid regions, of course, differ widely. Many animals have special means for enduring unusual and extreme temperatures. The reduction of the amount of water in an animal's body enables it

to tolerate wider ranges of variation; the evaporation of water from surfaces may cool the interior; the presence of coverings, such as lime and silica, apparently enables animals to endure greater extremes. There are instances where animals have gradually become acclimated to new ranges of temperature toleration when the temperature of their surroundings gradually changed. Dallinger (Davenport 1903) performed a classical series of experiments on protozoans. Starting with flagellates that were living at 15.6°C. and that died when the temperature reached 23°C., he gradually raised the temperature until the animals were living at 70°C. Such power of acclimation to new conditions makes it apparent how animals have become adapted to earth habitats. Welch and Loomis (1924) studied an enormous population of hydras in Douglas Lake, Michigan. When the surface stratum reached temperatures of 20–21°C. the hydras disappeared but remained in deep water at temperatures near freezing when the oxygen content was as low as 0.3 cc. per liter.

Growth and Reproduction in Relation to Temperature.—Temperature often exercises control over reproductive activities. Many littoral marine animals will not spawn until a certain temperature is reached (Chase 1935). In the Northern Hemisphere as spring advances a wave of gamete production passes northward. Egg production in many insects is less after exposure to low temperatures; variable temperatures in general increase the number of eggs produced, if they do not range beyond the usual limits of metabolic activity. *Planaria gonocephala* attains a particular maximum size at each temperature within its range and will not lay eggs until it has reached that size. When one is changed from a low to a high temperature, it does not lay eggs until it has grown to appropriate size (Abeloos 1929). The rate of development of poikilothermal animals varies more or less directly with temperature (Fig. 8; Krogh 1914), within ranges of toleration. The pupae of a mosquito, *Aedes togoi*, require 197 hours to complete their development at 8°C., 43 hours at 28°C., and 46 hours at 33°C., which is apparently above the optimum. The heartbeat of these pupae ceases at 4–6°C. and has a rate of 25.3 times per minute at 8°C., 140 at 37°C., and 107.6 at 39°C. (Yagi 1932). A flour-moth larva moults only four times when reared at 18°C. and five times at 25°C. (Gierke 1932). Japanese beetles reared at 20°C. produce smaller

adults than at 25°C. (Ludwig 1932). Some animals have different body forms at different temperatures. This is well illustrated by various plankton animals which bear long spinous processes when the water about them is warm and have short, stout bodies when it is cold. Such variations are of course related primarily to the viscosity and sustaining power of water, as it varies in temperature. In such animals as cladocerans and rotifers, temperatures influence sex ratios. In general, temperature exerts profound influences on reproductive activities.

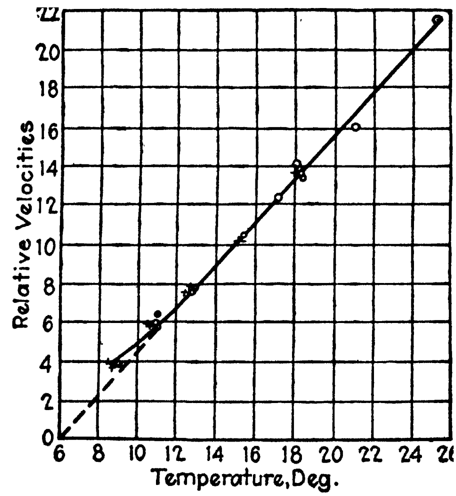


FIG. 8.—Graph of the temperature-velocity relationship of frog's eggs. (*From Chapman* 1931; *after Krogh* 1914.)

It influences or limits fecundity, rate and character of growth, size, form, etc.

Temperature and Genetics.—Studies on fruit flies (Drosophila) have demonstrated that temperature may affect the crossing over and somatic expression of gene characters. Certain characters show a greater percentage of crossing over (Fig. 9) at supra- and suboptimum temperatures (Plough 1917), and such effects may be induced by subjecting either males or females to unusual temperatures (Shull and Whittinghill 1934). The development of wings, eyes, and other characters may be influenced by keeping Drosophila larvae or pupae (Kerkis 1933) at high or low temperatures. Wings apparently tend to be longer at high temperatures and shorter at low temperatures (Riedel

1934, Stanley 1935). Zeleny and others have made important discoveries concerning the effects of temperature on the number of facets in Drosophila eyes. In general there is an increase in number at lower temperatures (Fig. 10). Bar-eye stock reared at 31°C. averaged 28 facets, and at 15°C. 189; normal-eye stock at 27°C. 700, and at 15°C. 900–1,000 (Krafka 1920). Temperatures to affect adults must act during certain periods of development which include only about a fourth of larval life (Luce 1935). Such modification of gene expression perhaps may be due to enzymatic action which increasingly inhibits facet formation at higher temperatures (Baron 1935). At high tem-

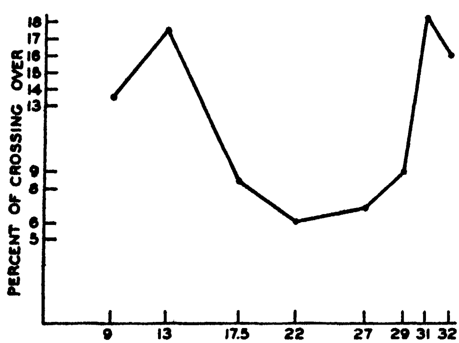


FIG. 9.—Effect of temperature on the crossing over of gene characters in Drosophila. (*After Plough* 1917.)

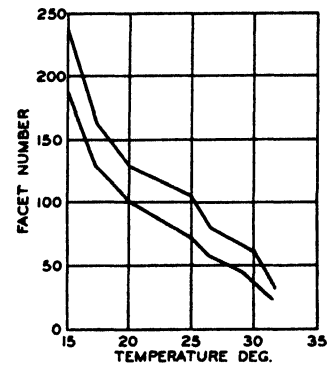


FIG. 10.—Temperature effect on facet number in males and females of bar-eye stock selected for low number in Drosophila. (*After Krafka* 1920.)

peratures broods of the insect *Harbrobracon* show increased homeosyngamy and decreased heterosyngamy (Anderson 1936).

Toleration of Low and High Temperatures.—Animals have optimum ranges of activity through which temperatures are favorable. Beyond these they become torpid or greatly excited and, if temperatures become too extreme, finally die. For example, Nieschulz (1935) has given a rather complete account of the activities of two species of flies, which differ somewhat in their adaptations to temperature. *Musca domestica* moves at 3.5–12°C. (average, 6.7°C.), is feebly active at 7.5–14 (10.8)°C., carries on normal activity at 15–22.5 (17.4)°C., shows increased activity at 24–34.5 (27.9)°C., manifests great restlessness at 37.5–42.5 (40.1)°C., goes into heat paralysis at 43.5–45.5

(44.6)°C., and dies at 45–47.5 (46.5)°C. *Fannia canalicularis* moves at 2–9 (4.2)°C., is feebly active at 5–16 (11.4)°C., normally active at 22–32 (25.5)°C., is very restless at 33–36.5 (34.3)°C., goes into heat paralysis at 36–40.5 (39.1), and dies at 37–42 (40.9)°C. In a graded temperature apparatus, Musca congregated between 20 and 40°C., but Fannia rested between 10 and 21°C. These two types of flies evidently have different optima and ranges of toleration for temperatures. A "vital optimum" is usually not one point on a temperature scale but a zone which extends through several degrees (Voute, 1935). Individuals in a particular species may show differences in toleration ranges, depending on the ranges of temperature to which they have been previously adjusted. The number of eye facets that may be induced by keeping Drosophila at various temperatures depends upon the temperatures at which the flies have previously been reared (Hersch 1924). The thermal death points of animals generally depend upon previous thermal experience; animals that have been kept at high temperatures can endure higher temperatures than those of the same species that have been kept at low temperatures, and vice versa. Ogle and Mills (1933) kept three groups of rabbits under different conditions. A lot kept for 6 weeks at 37–40°C. could endure high temperatures but had little ability to stand cold; the lot kept at 11–13°C. endured cold but succumbed readily to excessive heat. A third lot was kept warm for 16 and cold for 8 hours each day. Rabbits in this group were able to endure both heat and cold about as well as those in the other two lots. Ludwig (1933) subjected Drosophila pupae alternately to high and to low temperatures. When both temperatures were between the threshold and optimum there was no effect; if one temperature was between threshold and optimum there was acceleration in development; if both temperatures were outside the usual developmental range there was retardation. Variable temperatures have greater stimulating effects on sensation and metabolism of animals than those which are uniform. There appear to be strains of some species that have different temperature ranges. Payne (1934) described two strains of a flour moth (Ephestria) one of which had a life cycle twice as long as that of the other. The threshold of development for the slow strain was 8°C.; for the fast strain, 10°C. This moth could endure

temperatures between −15 and +50°C.; a braconid parasite which was associated with the moth survived when subjected to temperatures between −12 and +65°C. Undercooling in insects depends chiefly on capillary arrangement of water in tissues and is not a protective mechanism. Protection against cold depends largely on increase of bound water in tissues with decrease in temperature. Certain moss-inhabiting animals can survive temperatures as high as 150°C. and as low as −272°C., in liquid helium (Murphy 1938). Plants have germinated after being subjected to comparable low temperatures (Lipman 1936).

Effects of Low Temperatures on Animals.—Animals exposed to low temperatures may die of chilling before their protoplasm actually freezes. The formation of ice crystals in the body of an animal usually results in death. At low temperatures death may be brought about by direct mechanical injury, water loss through changes in permeability, or the precipitation of proteins and other irreversible chemical changes. There appears to be little chemical modification of protoplasm at low temperatures. Changes that slow metabolism and finally cause death probably are due largely to increases in viscosity and ice formation. Many animals can endure temperatures far below 0°C. without injury. The presence of salts, colloids, and other substances in body fluids of course lowers freezing points and thus protects from freezing. The elimination of water from tissues and body fluids serves the same functions (Payne 1926). Many animals when subjected to low temperatures eliminate water and prepare to hibernate. Ants do not do this and remain more or less active during winter (Dreyer 1938). "The smaller the animal, the more easily can it be super-cooled and the longer can this state be endured" (Kalabuchow 1935): turtle −5.3°, small bat −7.45°, bee −9.2°, and meal beetle −17.1°C. Some animals are specialized to endure prolonged exposure to low temperatures. Many escape the effects of chilling by providing insulation for their bodies or seeking refuge in situations where they will not actually freeze. Caterpillars commonly spin cocoons and pass the winter in a pupal state. Turtles and frogs hibernate in springs and on the muddy bottoms of ponds where temperatures may be low but not freezing.

Effects of High Temperatures on Animals.—When the temperature of an animal is raised beyond its limits of toleration, a

temporary heat rigor is induced. This may disappear if temperature is lowered or may be followed by death. After temporary heat rigor there may ensue *rigor mortis* which involves coagulation of proteins. Heat rigor appears in various animals at 26° to 60°C. or more, usually below 45°C. It is accompanied by changes in protoplasmic viscosity, permeability, and chemical composition. Water and salts in protoplasm generally increase sensitivity to high temperatures. Irradiation often strengthens the injurious effects of high temperatures which destroy enzymes, produce asphyxiation (especially in small, aquatic habitats), and cause other changes in animals and their environments. Animals that live locally or geographically in situations where they are not often subjected to high temperatures usually have little ability to endure them. Insects are usually less able to endure heat in dry than in moist air. Some aquatic (Coker 1935) and terrestrial animals aestivate at high temperatures. Animals that live in hot, dry habitats are often nocturnal or crepuscular. Many of them burrow or seek shelter where they can escape heat. Land animals have various mechanisms for cooling their bodies, usually largely by evaporation of water.

Light

Forms of Radiant Energy.—Radiant energy travels through empty space. That received on the earth comes largely from the sun, but it is emitted by every body that has a temperature above absolute zero. The growing parts of plants and physiologically active parts of plants and animals are believed by some scientists to emit weak mitogenic radiations (Rahn 1936). Radiant energy consists of waves or pulsations of different lengths which all travel at about the same velocity (3×10^{10} cm. per second) through space in straight lines. Radiation occurs over an extensive energy range. The short-wave, high-energy gamma rays penetrate several inches of lead; X rays pass through perhaps an eighth of an inch of lead; visible light is impeded by a metal layer only a few atoms thick; and long, radio waves are completely absorbed by a coarse copper-wire screen. Radiation may be observed only when it interacts with matter. It then shows such phenomena as reflection, absorption, refraction, and dispersion. There are three ways in which energy may be trans-

ferred with the aid of matter: (1) by the flow or movement of masses of matter, such as tides in seas or winds; (2) by wave motions in elastic media, as sound in air; and (3) by material projectiles. Radiant energy is transmitted as waves or pulsations. The wave theory of radiation assumes wave motion in an elastic medium (ether). It is supported by the fact that waves of all lengths travel at the same velocity and finds no difficulty with such phenomena as interference, reflection, refraction dispersion, polarization, and double refraction. However, it does not explain the emission and absorption of radiant energy satisfactorily, and the quantum theory does this better. When matter emits or absorbs radiant energy there is always rhythmical discontinuity in the process. "A given atom, for example,

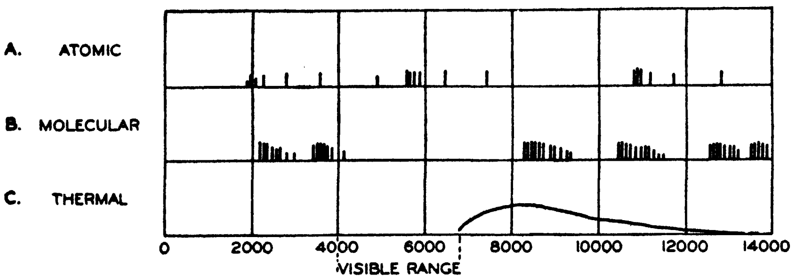


FIG. 11.—Comparison of ranges of atomic, molecular, and thermal radiations. (*After Rahn* 1936.)

will convert, of its store of energy, only certain multiples of the unit of energy into radiation. Likewise, it will absorb radiant energy only when energy comes in precisely the proper-sized amounts. This phenomenon is one with which the wave theory of light is unable to cope" (Rahn 1936). Energy is given off by atoms and molecules in excited states as pulses or rhythmical discharges. Radiant energy comes from hot bodies, chemical processes, electric currents passing through appropriate media, etc. A spectroscope shows types of radiation as bands which represent different wave lengths. Atomic radiation shows only certain lines, each associated with a certain energy; a molecular radiation usually shows groups of bands in particular regions; and thermal radiation gives a continuous strip which depends upon the temperature of the radiating body (Fig. 11). The length of radiations is measured in Ångström units (1Å = 10^{-10}m.) or millimicrons (mμ = 10^{-9}m.).

Effects of Light on Organisms.—Light, given direct access to protoplasm, generally causes injury by changing or breaking down compounds which are essential for life. It inhibits the growth of plants and animals, and they are adapted so as to be protected from it by the shielding of growing regions, the formation of pigment, etc. Light kills many plants and animals if they are exposed to it continuously, and those that live in strong light often have protective adaptations which enable them to survive. On the other hand, light is essential in most animal habitats because photosynthesis depends upon it, and without photosynthesis food resources fail. It has been well said that the cow is assimilated grass, and grass is sunlight, carbon dioxide, water, ammonia, and salt. Fish are assimilated algae, and algae are sunlight, carbon dioxide, water, ammonia, and salt. British scientists have been able roughtly to predict the catch of mackerel for a season by computing from the days of sunshine preceding. Irradiation increases the nutritional value of certain foods and may help to cure such food-deficiency diseases as rickets. Ergosterol when irradiated becomes vitamin D. Light in limited quantity may at times benefit protoplasm by virtue of the chemical changes that it causes—producing sterilizing effects or stimulating greater metabolic activity. Animals that live on the earth are always confronted by two horns of a dilemma—shun light because it is injurious, or seek light because it furnishes the energy for the production of organic food and certain beneficial chemical changes. Habitats have advantages and disadvantages as they afford too much or too little light, but light is not always beneficial or always injurious.

Light Variations in Environment.—Radiant energy varies with latitude, altitude, season, time of day, and humidity. The transparency of air and water is important in regulating the amount and quality of light that may be available in particular habitats. In water there is selective absorption of light at various depths; the longer vibrations are absorbed near the surface, and in general the shortest vibrations penetrate deepest. In the ocean, algae are distributed according to length of light vibrations that their colors are best suited to absorb and utilize: green algae live in the intertidal zone, brown algae descend somewhat deeper, and red algae are characteristic of deep water. Ditlevsen (1911) found that certain marine plankters in an

aquarium migrated from red to blue light. This, if light were used as a sign of organisms, would be equivalent to migration from shallow to deep water. Some animals carry algae on or within their bodies and depend on them more or less for food. These are limited to shallow waters because the enslaved algae cannot manufacture food in the absence of sunlight. Greider and Downes (1931) found that antirachitic ultraviolet rays, as judged by physical measurements, at an altitude of 6,000 feet were five times as intense in summer and 2.5 times in winter as they were at 1,000 ft. Cosmic rays also increase at high altitudes. Rickets is rare in the tropics, probably because ultraviolet rays are more prevalent than in temperate regions (Coblenz 1935). The number of hours of sunshine there is more uniform throughout the year, and in winter does not pass such long distances through the atmosphere, as in higher latitudes. The local distribution of types of plants and animals may depend on the illumination of sloping land surfaces. The trees on the north and south sides of a mountain are often quite different. The distribution and abundance of certain species of algae and barnacles on rocky beaches depend on whether walls are shaded or illuminated. In soil the oxidation of substances to make nitrates and nitrites available for plants takes place much more rapidly when soil is illuminated than when it is in darkness. High soil temperatures in the tropics (50°C.) are favorable for photooxidation but above optimum for nitrification by bacteria (Dhar 1935).

Photic Stimulation.—The stimulating effects of light are apparent in the physiology and behavior of animals. Pigment formation is due to light in many cases—the flounder has under experimental conditions been made to form pigment on the upper, lower, or both sides, according to the illumination to which its body was subjected. Pigments are frequently arranged in such patterns that animals match the backgrounds on which they usually rest. Such protective resemblance would not be possible without light. Animals that live in caves lack pigment, and those that dwell in the depths of the ocean, where the environment is monotone, though pigmented, do not show patterns in their coloration.

Light influences the behavior of animals in many ways. There are certain species, attuned to low intensities, that are well-known

as nocturnal or crepuscular animals; others that are as characteristically diurnal. Some animals, like leeches, chase shadows; others, like hermit crabs, avoid them. Sunlight is said to be the most potent factor that induces bees to go afield in search of honey. The stimulating effects of light may be due to various wave lengths, and it is probable that light produces chemical changes when it stimulates, but there is apparently no direct relation between chemical effect and the degree of stimulation. Ultraviolet light is potent chemically but is invisible to the human eye. Bertholf (1932) has studied the stimulating effects of light in different spectral zones on the movement of flies. The efficiency is very low for the long-wave lengths but begins to rise at about 575 mμ and reaches a maximum in the "visible" at 478 mμ. It then decreases as far as 425 mμ, then rises suddenly to an efficiency at 365 which is over five times as great at any point in the visible. From here it decreases rather constantly. The shortest wave length at which a response was observed was 235 mμ; the longest, 550 mμ. Bertholf concludes that fluorescence cannot account entirely for the great potency of ultraviolet rays. Colors in relation to animals have been discussed in Chapter III.

Diurnal Light Variations.—The rotation of the earth on its axis has led to many adaptations in animals. Perhaps the most striking examples are in animals that are strongly diurnal or nocturnal and in the migrations of plankton. That light has a direct photokinetic effect on some animals is shown by the fact that many animals assume sleeping positions during an eclipse, instead of remaining active as they would if light continued as usual (Wheeler *et al.* 1935). The migratory locust is said to stop its flight at once if the sun goes behind a cloud. Young eels, migrating up streams, stop and hide at night. There are some organisms, however, that appear to have an established physiological rhythm which continues for a time even when the alternating conditions of illumination that go with day and night are not present. Acacia leaves continue to assume "sleeping" positions at regular intervals in the absence of light. The shrimp, *Hippolyte varians*, continued to turn green, which is its usual night color, at rather regular intervals when it was kept continuously in light or dark (Keeble and Gamble 1900). Everyone knows that certain animals are adapted to activity during

light and that others are adapted to activity during comparative dark. Many birds go to roost when night falls. Rats are active at night (Browman 1937). Some fishes, like a trout, take food only during the day; others, like a bullhead, seek food at night. Cave animals commonly have degenerate eyes or are actually blind, but nocturnal animals often have very large eyes—vertebrates frequently showing vertically elongated pupils, and insects having eyes with very large facets. Graenicher (1911) describes a species of nocturnal bee in which the female is flightless, creeping over the ground, and has normal eyes, but the male, which flies, has eyes with enormous facets. Some animals that become active at night do not do so on account of the reduced amount of light but on account of other conditions prevailing at that time. Nighthawks fly when they can catch insects and, although they are usually seen at dusk, may fly during the day if food is abundant. Land snails become active when there is plenty of moisture, which is usually, but not always, at night. The larvae of the filarial worm, *Wuchureria bancrofti*, are present in the blood of man at night and are thus adapted to transmission by mosquitoes; but if the man sleeps during the day and works at night, the larvae appear during the day. Their appearance is not correlated with light but with the condition of their host. The increase of periods of daylight in spring stimulates the development of gonads (Benoit 1935) and seasonal migrations (Rowan 1931) of birds, and shortens the life cycles of insects (Baker 1935). Plants and animals fall into three classes in regard to sexual activity in relation to light: (1) active with an increasing daily period or intensity of light of certain wave lengths, (2) active when light decreases, and (3) without evident photoperiodicity (Bissonnette 1936).

Plankton Migrations.—Many species of plankton animals in the ocean and in lakes make periodic migrations, coming to the surface at night and descending into deep water during the day. Light is doubtless the controlling factor in such migrations, but is not the sole factor that operates to produce them, and does not by its presence or absence cause plankters to move immediately toward or away from the surface. One species of crustacean comes up at sundown and leaves before midnight; another comes up at midnight and goes down at two o'clock in the morning, before the faintest dawn has appeared. Each species is

adjusted in its own particular way to the daily rhythm. Ewald (1912) found that cladocerans became adapted to new light intensities rapidly; that increases in intensity made them positively, and decreases negatively, phototropic. He believes that plankton migrations are wholly explained by the responses of the animals concerned to light.

Seasonal Variations in Light.—The seasonal variations in light have a marked influence on the animals in frigid and temperate regions. Such variations are, of course, always associated with corresponding differences in temperatures. Summer is a season of comparative warmth, intense illumination, and great photosynthetic activity; winter brings cold, scanty illumination, and lowered metabolic activity. British scientists have shown that light has an effect that may be independent of temperature. Sunshine in May brings an abundance of marine copepods and a good catch of mackerel, regardless of whether the seasonal temperatures are low or high.

Light and Genetic Characters.—Light, like temperature, may influence the manifestation of genetic characters and modify reproduction. Shull (1928) has shown that aphids reared in continuous light are wingless and in continuous dark mostly wingless, but in alternating dark and light the proportion of winged individuals is related to length of exposure to light. Such differences are not due to food. The determination of wing condition is apparently 16 to 34 hours before an aphid is born. The maximum number of winged individuals was induced when 6.25 hours of light alternated with 12.5 hours of dark (Shull 1929). Sex was correlated with wing production, for there were more males when there were more wings.

Luminescent Animals.—Throughout the animal kingdom there are animals that produce light. The best known forms are the dinoflagellates (Noctiluca), hydroids, jellyfishes, ctenophores, sea pens, Chaetopterus and other marine worms, earthworms, brittle stars, various crustaceans, myriapods, fireflies and glowworms, *Pholas dactylus* and *Phyllirrhoe bucephala* (both molluscs), squids, Pyrosoma (a colonial ascidian), and fishes (Harvey 1920). All these animals are marine or terrestrial, no luminescent animals being known to inhabit freshwater. The eggs and larvae of some animals (firefly) are luminous. In some animals bacteria serve as a source of light; a fish has been reported that bears

cultural pores for bacteria. All luminescence emanating from animals is associated with oxidation. Most luminescent organs flash only when stimulated; fireflies flash when there are loud explosions (Rudemann 1937). Harvey divides such organs into two classes: (1) those in which oxidizable material is included within cells and (2) those in which it is burned outside the cell substance. Some light-producing organs are constructed somewhat like eyes, with lenses, screens, etc. Luminescence is often under nervous control; even colonial animals, like Renilla, may show flashes over a whole group of animals at the same time. Groups of fireflies (Photinus) often flash rhythmically and in unison (Morse 1916, 1918). In some animals luminescence is a periodic phenomenon, and in such instances light is usually given off at night. Some animals are luminescent only during the breeding season.

Harvey believes that luminescence is brought about by the action of luciferase, an enzyme, on luciferin, a protein substance which has various forms, in the presence of oxygen. The light from luminescent animals is usually of low intensity, that of the firefly having a strength of 0.02 to 0.0025 candle meters. The light from animals is peculiar in having a spectrum similar to that of luminescent chemicals. It appears only at certain temperatures which vary in different species of animals. That from the firefly will, like X rays, pass through wood, paper, leather, and flesh in sufficient quantity to affect a photographic plate, but such "invisible" rays, like ultraviolet light, will not penetrate glass.

Various functions have been assigned to luminescence in animals (McDermott 1912). Such light undoubtedly serves as a signal for recognition and perhaps also in keeping schools of marine animals together. It is used as a lure for attracting prey by certain angler fishes and coelenterates. It may serve as a lantern and as a warning to predaceous enemies. Brown (1926) has reported a spider which emits light when disturbed. Fireflies are distasteful to some predaceous animals, and their flashing may give warning of undesirable qualities to bats and other predators. In many organisms luminescence apparently serves no useful function—as in certain bacteria, fungi, protozoans, coelenterates, firefly eggs, and larvae. Some luminescent animals are blind; and others have photogenic organs in peculiar

situations where use seems doubtful, as in the case of a deep-sea crustacean that has luminescent organs inside its branchial chamber.

MEDIA

The chief media in which animals live are of course air, water, and soil. All these are subject to variation in their constituents. Some animals are able to exist in very peculiar media; many have taken up abodes within plants and animals. Nematodes live in vinegar. Flies of the genus Psilopa flourish in petroleum (Thorpe 1930, 1931). Other fly larvae survive when submerged in absolute alcohol (Cameron 1911). Certain mosquito larvae live in concentrated sea water which has a salinity twice that of the open sea (Pearse 1932, King & del Rosario 1935).

Extent of Media.—Everyone knows that large aquatic animals, such as big fishes and whales, are characteristic of great rivers and wide oceans; little puddles and standing water in holes in tree trunks support protozoans, tardigrades, and mosquito larvae. Long ago Semper (1881) pointed out that the size of certain species of animals depends upon the extent of the body of medium in which they live. Snails reared in small dishes do not attain the size of those of the same species grown in large containers. When animals live in limited amounts of media they may be poisoned by their own excretory products, be unable to obtain sufficient or adequate variety of food, suffer from lack of exercise, crowd each other, be unable to reproduce, or be subject to injury in other ways. Small habitats are usually monotonous, and conditions in them are easily changed. Media of large extent usually contain a variety of conditions and can absorb minor variations in factors without being much changed.

The Atmosphere

Composition of Atmosphere.—The atmosphere constitutes about 1/1,200,000 of the earth's mass. It is made up largely of oxygen and nitrogen in the proportion of 21 to 79 parts by volume. These two gases are not chemically combined but thoroughly and uniformly mixed the world over. Nitrogen is rather inert chemically, but oxygen readily combines with many substances in the earth's crust and in the bodies of living organisms. Ordinary atmosphere, in addition to nitrogen and oxygen,

contains about 0.03 per cent of carbon dioxide; water vapor; dust particles; bacteria; pollen grains; spores; sea salt; rarer gases such as helium and neon; and even at times, after electrical discharges, such substances as ammonia, nitrous acid, and ozone. Though carbon dioxide occurs in small quantities, it serves an important function as one of the basic substances for the manufacture of carbohydrates by photosynthesis in green plants. Animals that breathe in the atmosphere usually find ample oxygen for their respiratory needs. But sometimes carbon dioxide, which is heavier than oxygen, accumulates in holes, especially in mines and caves, and may even suffocate animals. It is produced by respiration, combustion, and other processes in which oxidation is involved. There may be as many as 400,000 dust particles per cubic centimeter. These may serve as nuclei for the formation of fog, mist, rain, snow, and hail.

Atmosphere as a Home for Organisms.—No plants or animals live permanently in the atmosphere, continually above and separate from the earth's crust. However, its transparency and low density make the atmosphere an excellent highway for animals and plants that move from place to place. The air currents and vortices that keep dust particles suspended and help sustain flying animals, transport small animals, pollen grains, and seeds (Felt & Chamberlain 1935, Felt 1937). Some plants and animals are spoken of as "aerial" because they spend much or all of their time above the earth. Buzzards and frigate birds soar hour after hour, constantly scanning the earth's surface for prey. Some epiphytes spend their lives suspended high on the trunks of trees. Winds help aerial transportation. They also change surface habitats by carrying dust and moisture and by moving solid bodies. They also change earth contours by producing waves and currents in bodies of water. These exert more force for transportation of objects or pounding on surfaces because of the greater mass of moving liquids. In general, winds and flowing waters tend to reduce elevations of land to base level. Thus they help to fill low places and erode high places.

The Atmosphere and Weather.—Climate has been discussed briefly in Chapter II. The atmosphere serves the earth as a thermal blanket. Especially when it is moisture-laden does it impede radiation from the earth's surface and thus prevent rapid

changes in temperature. The ionization of air as well as its humidity is believed to influence the response of animals to weather. High electric conductivity of air rather than high humidity may be responsible for certain responses of animals to climatic changes (Ceresole 1932). Humidity apparently affects the development of insects very little, but variations in temperature do (Rivnay 1935, Ulyett 1936). An insect loses very little water through its exoskeleton but much through its respiratory system (Mellanby 1935, 1936). Cocoons impede evaporation or water absorption but do not prevent temperature changes within them. The great changes in the effectiveness of solar radiation in

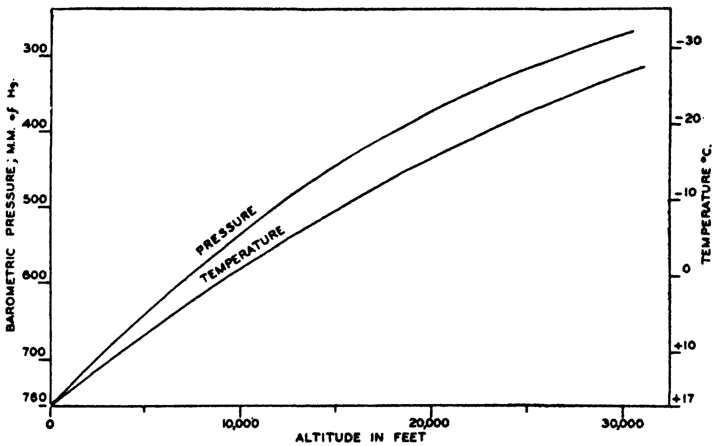


FIG. 12.—Temperatures and pressures at various altitudes.

high latitudes with seasonal procession are due in part to the fact that rays at certain times shine directly through the atmosphere and at other times must take an oblique course and therefore travel much farther through air.

Altitude and Atmosphere.—In going away from the surface of the earth the atmosphere becomes rarer and cooler (Fig. 12). The decrease near the earth is roughly about 1.0°C. and 5.1 mm. of pressure as measured by a column of mercury for each 200 m. of elevation (1.0°F. per 365 ft.; 1 in. per 1,000 ft.). On account of such differences, high mountains usually have more or less permanent belts of clouds near their summits and may be surmounted by a perennial snowcap. In the tropics there may be as many as five zones on the sides of a single mountain: (1) tropi-

cal; (2) warm temperate, with clearly defined summer and winter seasons; (3) cool temperate, where trees shed their leaves in winter and at the top of the zone cease to grow altogether; (4) cold, where trees are absent, but grasses, other hardy herbs, mosses, and lichens persist; and (5) frigid, with its lower limit at snow line. In the limitation of animals to definite zones, temperature and available moisture are probably more important than variations in air pressure. However, barometric pressure at 10,000 ft. is only about two-thirds that at sea level, and the amount of oxygen is less. Certain insects can endure pressures that vary rapidly from 760–0.0001 mm. of mercury (Lutz 1929). Some animals are unable to ascend to high altitudes because the decreased oxygen pressure does not permit aeration of their blood; others are able to change from one altitude to another with impunity. Land animals naturally living at high altitudes have blood that has greater affinity for oxygen than the blood of those in the lowlands. Such animals as the llama and vicuna are able to live and remain active in an environment quite deficient in oxygen. "The ability of haemoglobin to carry oxygen seems to account in part for adaptations of certain birds and mammals to high altitudes" (Hall 1936). The physiology of animals at high altitudes has been summarized by Gildenmeister (1932). There are changes in blood, lymph, circulation, respiration (Hurtado 1932), general metabolism, temperature regulation, acid-base equilibrium, skin, and nerves. The change in the quality of solar radiation with increasing altitude makes alpine sunlight favorable for the treatment of certain diseases.

Water

Water as a Constituent of the Earth.—Although water constitutes only $\frac{1}{4540}$ of the earth's mass, it covers about 72 per cent of the earth's surface and would, if uniformly distributed, form an ocean about two miles deep. From the whole surface of the sea, water to a depth of nearly a meter evaporates annually, and at the equator more than two meters everywhere passes from it into the atmosphere. Thus a hydrologic cycle begins (Fig. 17). Water vapor is transferred to all parts of the earth and precipitated as dew, fog, rain, snow, and hail and thus supplies regions far distant from oceans. Considerable water is also vaporized from land surfaces. About 6,500 cu. miles runs

off the land through streams annually. This carries some 5 trillion tons of dissolved and suspended matter with it. So all chemical elements are transported to the oceans, though some, of course, occur in minute quantities.

Characteristics of Water.—Water occurs in several forms on the earth. Above 100°C. it exists largely as monohydrol, in the form of vapor or steam; below 0°C. it is largely trihydrol, or ice; between 0 and 100°C. it is usually a liquid which contains varying amounts of mono-, di-, and trihydrol, according to its temperature and recent history, and is continuously losing monohydrol to the atmosphere. In other words, water is a mixture of various highly polymerized types: (H_2O), $(H_2O)_2$, $(H_2O)_3$, etc. Liquid water that has just been condensed from vapor contains little trihydrol, whereas that which has recently been formed by melting ice contains much. Besides polymers, water is further complicated by the occurrence of heavy and light isotopes of hydrogen and oxygen in the water molecule. Heavy water, or deuterium oxide (D_2O), contains a heavier atom than ordinary water (H_2O). Recent work indicates that the presence of trihydrol is favorable to certain biological processes and that deuterium generally tends to retard such reactions (Barnes and Jahn 1934, Barbour 1937). It has even been suggested that cold oceans teem with life, at least in part, because they contain much trihydrol; whereas warm, tropical oceans support less life because they have more of other forms of water. As a medium in which animals may live, water offers many advantages. It has buoyancy and thermal stability and is an almost universal solvent. Its pressure and viscosity vary with depth and temperature. Compared to the atmosphere, it contains less available oxygen for respiratory processes and because of its greater density will not permit such rapid locomotion.

Water in Relation to Temperature.—The high specific heat of water is a unique and biologically important property. It is due largely to the heat of dissociation of trihydrol. Aquatic habitats are thermally quite stable because water changes temperature comparatively slowly. In the atmosphere the evaporation of water requires heat and thus cools surrounding bodies; as vapor, water carries latent heat which is released when it condenses. Land areas near large bodies of water have equable climates because water does not permit rapid thermal variations.

Water vapor in the atmosphere also operates against sudden changes. It serves as a thermal blanket which prevents rapid radiation from soil at night or at other times when there is no sunshine. The control of evaporation from the surfaces of the bodies of land animals helps in conservation or dissipation of heat.

Water as a Solvent.—No other liquid is capable of dissolving so many substances as is water. Except for its hydrolytic and electrolytic effects, water acts upon its solutes very little and is, therefore, an excellent carrier for a great variety of substances. The remarkable solvent capacity of water gives it certain inherent advantages and disadvantages as a medium in which animals may live. There is a relation between temperature and the solvent capacity of water. In general, larger quantities of solids can be dissolved at high temperatures, and more of gases at lower temperatures. When water nears its freezing point, salts tend to precipitate out; when it nears its boiling point, gases tend to pass out of solution. Carbon dioxide in water tends to combine with it, and thus a weak acid is produced. Many substances that are readily soluble in water are poisonous and may kill aquatic animals; other dissolved substances are of value because they furnish materials for nutrition. Water has an intimate relation with living matter, which is so largely made up of it. Protoplasm readily combines with water and may take in or lose it without changing its essential character. A part of the peculiar properties of life lies in the ability of protoplasm and water to mix with and form various more or less stable compounds with each other.

Density, Surface Tension, Viscosity, and Pressure of Water.—Water becomes more dense and viscous at lower temperatures. This gives greater buoyancy. Aquatic animals are usually slightly heavier than water, and they sink more readily in less dense water. Many animals change their forms as the buoyancy of water varies with changing seasons. When water is dense and viscous they have compact bodies, but when warm water has less power to hold them up, their bodies bear long spines or other organs which impede sinking. Compact "winter" forms and attenuated or spinose "summer" forms are known among various species of protozoans, rotifers, and crustaceans (Fig. 13). In passing from shallow to deep water, pressure increases. At great depths it may be several tons per square inch, depending

on the weight of the column of water above. As pressure increases, certain substances become more soluble. Water under pressure will hold more gas or salt in solution. Carbonated water must be kept under pressure, or it will lose its charge. Lime deposits decrease at great depths in the sea because more lime is held in solution as pressure increases. There is evidence that increase in hydrostatic pressure causes a decrease in the viscosity of protoplasm (Brown & Marsland 1936). Cattell (1936) has reviewed the physiological effects of high hydrostatic pressure. Some animals, like water striders, depend on surface

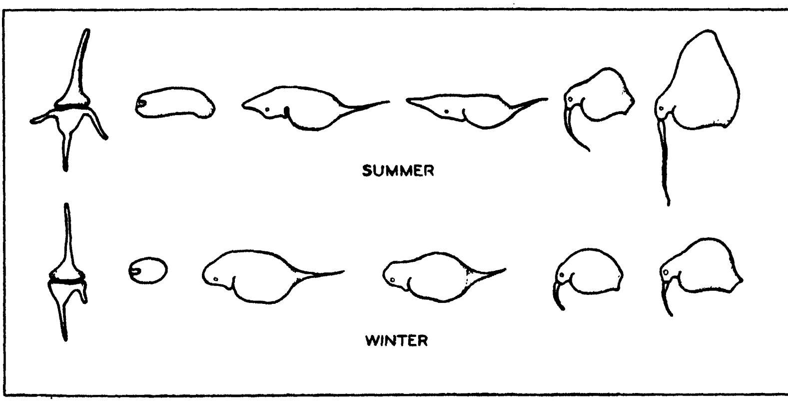


FIG. 13.—Summer and winter forms of a protozoan, a rotifer, and four species of crustaceans. (*After Wesenberg-Lund* 1911.)

tension to keep them on top of water films; others (snails, etc.) crawl about below such films.

Gases in Water.—Aquatic animals that secure their oxygen from water are at a disadvantage compared to land animals, because the atmosphere almost always contains about 21 per cent of oxygen, whereas oxygen in fresh water saturated with dissolved atmospheric gas varies from 10.29 cc. per liter at 0°C. to 5.57 at 30°C. and 0.0 at 100°C. With increase in salinity, oxygen becomes somewhat less. In sea water which contains 20 g. of salt per liter there will be 7.97 cc. of oxygen per liter at 0°C. and 4.46 at 30°C. Where there is stagnation, and oxygen is used up by respiration, putrefaction, or other oxidative processes, oxygen may fall much below saturation or even be absent altogether. The swim bladder of certain fishes serves both as a hydrostatic organ and as a storage reservoir for oxygen. When

a fish enters a deep stratum in a lake that is deficient in oxygen, an increase in carbon dioxide in the swim bladder causes pressure in the bladder to increase, and the fish rises to a higher level where it will be in aerated water (Hall 1924). Nitrogen in water is inert and has little influence on organic processes. It of course varies in amount with changes in temperature; hydrostatic pressure may even cause nitrogen to supersaturate water when it is brought to higher levels because pressure is decreased. Carbon dioxide occurs free, combined with water to form carbonic acid, and in salts as carbonates (fixed) or acid (half-bound, or bi-) carbonates. Free or half-bound carbon dioxide may be used by plants for photosynthesis, but fixed carbon dioxide is not available. In alkaline water all carbon dioxide may be combined, but in acid water as much as 30–49 cc. per liter may be present, and such water will effervesce when brought from cool depths and exposed in air. Photosynthesis may produce an excess of oxygen so that water may at times be supersaturated; respiration, putrefaction, and similar oxidative processes may also cause supersaturation with carbon dioxide. Methane results from the slow decay of organic matter. It is often called "marsh gas" and is characteristic above muddy bottoms. Hydrogen sulphide is found in similar situations. Some animals live and remain active in water that is free from oxygen for two or three months each year. Cole (1921) believes that such animals obtain oxygen through the action of an oxydase on decomposing plant remains.

Salinity.—Dissolved salts in water are of great importance in animal environments. The chief differences between salts in the sea and freshwater are shown in Table 2 (adapted from Baldwin 1937, p. 7). The open sea contains more than a hundred times as much salt as ordinary freshwaters. Animals that spawn in the latter must therefore provide salts in their eggs for the needs of developing embryos, but the developmental stages of marine animals can readily absorb salts from the water around them. Some adult animals can migrate readily from sea to freshwater, but their eggs cannot develop in the latter, and their distribution is thus limited. Freshwater, furthermore, has a relatively high carbonate content and little chlorine. Through millions of years the hydrologic cycle has been transporting chlorides to the ocean, but carbonates are continually being formed over land areas. The sea has gradually grown saltier.

The plants and animals in the sea have influenced its composition. As an environment the sea is in part a product of the organisms in it. Some elements have been fixed, and others discarded (Irving 1936). In estuaries and marshes near the sea, animals and plants are often arranged in zones, according to their ability to tolerate sea water or dilutions of it. Even such delicate animals as jellyfishes are able to endure dilutions that contain only 30 per cent of sea water (Benazzi 1933). From freshwater, hardy insects (such as certain flies, bugs, and beetles) quickly invade brackish waters. Mosquito larvae live in pools of concentrated sea water in salinities as high as 8.8 per cent (King & del Rosario 1935). Most freshwater fishes show little toleration for salt. Some marine animals have after many thousands of

TABLE 2.—COMPOSITION OF SOME TYPICAL NATURAL WATERS IN GRAMS PER LITER

	Na	K	Ca	Mg	Cl	SO_4	CO_3	Total
Sea water.........	10.7	0.39	0.42	1.31	19.3	2.69	0.73	34.883
Hard fresh water...	0.021	0.016	0.065	0.014	0.041	0.025	0.119	0.301
Soft fresh water....	0.016	.....	0.010	0.00053	0.019	0.007	0.012	0.065

years entered freshwater, but on the whole such migrants have been few, and more have gone directly over ocean beaches to land (Pearse 1936). Not only is the total amount of salt in a medium significant in the lives of animals, but particular salts, radicals, and elements may act as depressors or excitants or exert influences that are beneficial or injurious. Salts of copper, mercury, and arsenic, for example, are usually poisonous above certain minimum quantities. Commercial wastes often pollute aquatic habitats so that animals are unable to live in them. Such compounds as nitrates, phosphates, and silicates often show seasonal variations in amount and may limit productivity. One factor that impedes the migration of marine animals into freshwater is that respiration is more difficult as salinity decreases (Beadle 1931, Schleiper 1933). The body fluids of many marine animals are much like the medium that surrounds them, but those of marine teleosts are hypotonic to sea water and not very different from the fluids in their relatives in freshwater. Some crustaceans are more or less homeosmotic, but most are poikil-

osmotic, *i.e.*, the former have mechanisms for maintaining nearly constant salinity in body fluids, but the latter have little or no resistance to the passage of salts through their external membranes, and their body fluids are therefore much like those in the surrounding medium (Pearse 1936). Crabs show a general reduction of the salts in their bloods as they migrate from sea to land (Pearse 1932).

Osmotic Pressure.—The phenomena of life in plants or animals are closely associated with the passage of liquids and gases through membranes. An animal has two lines of defense, so to speak, in regulating the passage of fluids into or from its body:

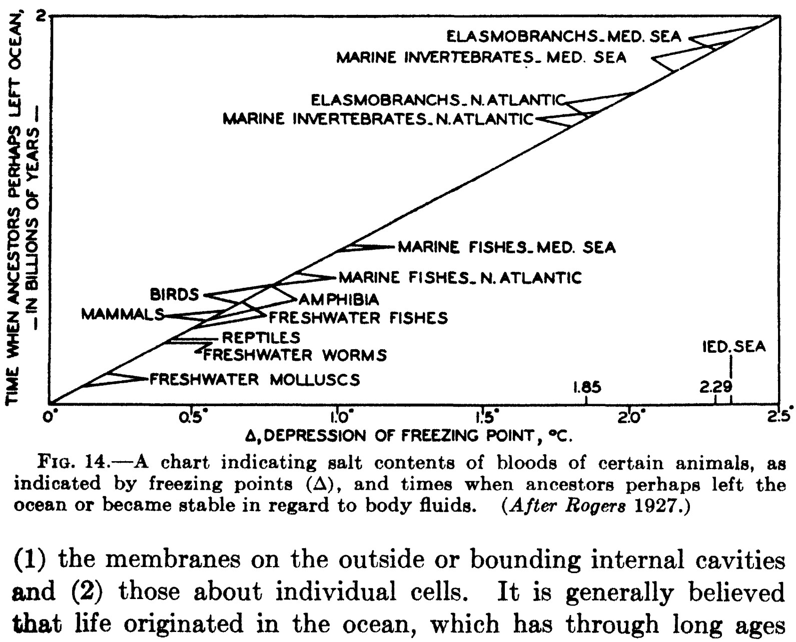


FIG. 14.—A chart indicating salt contents of bloods of certain animals, as indicated by freezing points (Δ), and times when ancestors perhaps left the ocean or became stable in regard to body fluids. (*After Rogers* 1927.)

(1) the membranes on the outside or bounding internal cavities and (2) those about individual cells. It is generally believed that life originated in the ocean, which has through long ages grown more saline. As the body fluids of many marine invertebrates today closely resemble sea water, and as those of all animals have a general resemblance to that great and old medium for life, it is often said that "blood is modified sea water." Rogers (1927) gives a good exposition of this view and presents a scheme (Fig. 14) that he believes to indicate roughly the relative time when various animals left the ocean, as indicated by blood salinity of living representatives. The problem of an animal in freshwater is to keep up the salt concentration within

its body; it is hypertonic to its surrounding medium. On the other hand, an animal in the ocean may be nearly isotonic with its medium or hypotonic to it. Its problem is to secure water and eliminate salt. Marine teleosts excrete salt through their gill membranes. Aquatic animals fall into three groups in their relations to the medium in which they live: (1) some have little or no control over the passage of solutions through their membranes and are nearly isotonic with the surrounding medium; (2) others can control to a considerable degree the passage of solutions through their membranes and maintain a comparatively steady physiological state by active regulatory mechanisms but are influenced by changes in the medium; (3) others have external membranes which are practically impervious to solutions, and their internal liquids are maintained in a relatively stable state through various internal regulatory mechanisms. The body fluids of marine invertebrates, cyclostomes, and elasmobranchs have an osmotic pressure slightly greater than that of the sea water about them; freshwater invertebrates are hypertonic to their medium; bloods of freshwater fishes, amphibians, and reptiles are much like those of mammals. Kidneys were perhaps developed first to eliminate metabolic waste products and have some ability to select particular substances for excretion, but some marine animals of rather complex structure (echinoderms) have none. Kidneys also have differentiated a function of eliminating excess water. Sea water is a balanced solution. If its composition is varied, plants and animals will not live. In it sodium acts on living membranes to maintain osmotic pressure and stimulate cells, and in excess it poisons cell membranes; potassium neutralizes the effects of calcium ions, is radioactive, and influences the speed of responses; calcium is antagonistic to sodium, preserves cell membranes, and thus regulates permeability. In general there has been evolution among animals toward osmotic independence. All vertebrates can maintain an osmotic gradient with the medium around them. Baldwin (1937) says:

Summing up the case of the fishes, it seems we can say that they all originated in fresh water. The presence of a water-secreting device in the form of the glomerulus is evidence of fresh-water ancestry. The glomerulus degenerated in those teleosts which went to sea, in response to the necessity of conserving water as much as possible but it persisted

in the elasmobranchs for these forms found in physiological uraemia an alternative method of protecting themselves against loss of water. Some of these forms have recently returned to fresh water, and though they still show the phenomenon of uraemia for other reasons, the degree of uraemia has been greatly reduced in response to the change in osmotic conditions to which they are exposed.

Ionization.—Electrolytes in solution tend to split up into ions, and these have marked effects upon water as a medium for life. Sea water contains a complex mixture of partially ionized salts, and each of these has specific properties. Even distilled water tends to break up into hydrogen and hydroxyl-ions. In natural waters trends toward alkaline reaction are due to salts, and "acid" waters are generally produced by carbon dioxide, though complex organic acids (humic, tannic, etc.) may contribute. In the ocean carbon dioxide is driven out as temperature rises and alkalinity increases; the opposite is true when temperature falls. Bottom fishes and those associated with vegetation have been observed to show little response to variations in ionization, but those which frequent open waters may react very quickly to such changes. In acid soils drying produces little change in ionization, but drying alkaline soils makes them less alkaline by changing hydrogen-ion concentrations (Burgess 1922). It appears to be generally true that aquatic animals under natural conditions are usually not markedly influenced by ions in their environments. Most species tolerate quite a wide range, and ions do not often cause animals to select or reject particular habitats. For example, Young (1936) after carefully studying the effects of solutions concludes that "osmosis is a more important factor in the lives of fishes than is exact balance of ions," but some degree of balance is necessary. The body fluids of animals are generally slightly alkaline, and, when chemical processes tend to produce acidosis, buffer substances bring them back toward neutrality. Buffers are salts of weak acids (HCO_3, HPO_4, etc.) which are readily split up. Through the membranes on the surfaces of aquatic animals there is a continual passage of materials. Excretory organs pass substances out, and other membranes permit ions, salts, and other substances to enter. Even when an aquatic organism has attained a steady state in a comparatively stable environment active work is necessary by surface membranes to maintain such a state (Pantin 1931). As long as an animal

lives it maintains a gradient between its body fluids and the surrounding medium. Though the fluids in animals resemble sea water, they always differ somewhat. In the physiology of animals electrolytes play an important role through the control of enzymatic action and permeability. Life is perhaps concerned as much with the passage of liquids through membranes as with anything. Membranes that bound exterior surfaces and separate internal structures are therefore of prime importance. Baldwin (1937) attributes the "differences between external and internal media to differences in ionic mobilities, exaggerated by the presence of negative charges on the boundary membranes, the whole effect being called into play by the activity of the excretory organ." Potassium ions move faster through membranes than sodium ions, and sodium ions move faster than magnesium ions. So body fluids contain more of potassium and less of magnesium than the external medium. In passing from simple to more complex animals the greater becomes the relative excess of potassium and the relative deficiency of magnesium.

Organic Compounds in Water.—Organic substances in water may be beneficial or injurious; they may act as foods or toxins. Certain species of mosquitoes will not lay eggs in water that is uncontaminated with organic matter (Buxton and Hopkins 1927, Beattie 1932), and some can grow from egg to adult with no food except dissolved and colloidal organic substances (Hinman 1932). Water that has been "conditioned" by having animals kept in it may promote growth of or injure other animals. Fishes kept in water that had previously contained clams grew faster than those kept in unconditioned water from the same source (Allee, Bowen, Welty, & Oesting 1934). In similar experiments Shaw (1932) found that fishes and salamander larvae often showed greater growth and regeneration in conditioned waters. In general, heterotypic conditioning was more effective than homotypic conditioning, which at times was injurious. Some animals flourish in highly contaminated waters, such as those from sewage-disposal plants. In Guadeloupe, Bonnet (1932) observed a fish (*Lebistes reticulatus*) living in enormous numbers in stagnant sewer waters, where in milligrams per liter there was organic matter 32, sulfur 2, free ammonia 5.8, albuminoid ammonia 7.8, and chlorides 655. Freshwater ciliates usually have wide toleration for temperature, oxygen, carbon dioxide, and pH and are

distributed where food is available (Noland 1925). The value of dissolved organic substances as food for aquatic animals will be discussed more fully in the section on nutrition. The discharge of wastes from factories and mills often makes it impossible for animals to live in waters that receive them. Surrounded by the contaminated medium, animals cannot escape. The most resistant are chitin-covered, active, air-breathing insect larvae, such as those of *Chaoborus punctipennis*, which is often the only animal that survives in contaminated reservoirs. Oils from vessels often kill sea birds by decreasing the insulating properties of feathers and thus lowering body temperature (Porter & Raffy 1934). The waste products of animals are often injurious to others in small bodies of water, but certain animals use such excremental materials as food.

Humidity.—One of the prime factors in determining climate is water in the earth's atmosphere. The distribution of terrestrial plants and animals depends largely on this. Plants are commonly classified according to their water requirements as hydrophytes, mesophytes, and xerophytes; and their ability to fit environment depends on atmospheric as well as soil water. The plant cover of the earth also absorbs water from atmosphere and soil and retards the runoff of precipitated water. During transpiration, plants give off water vapor and thus humidify the air. Large bodies of water make the climate of neighboring land areas more stable because humid air changes temperature slowly and serves as a thermal blanket over the earth. Dry climates often show marked diurnal and seasonal changes in temperature.

Water in the Atmosphere.—From the atmosphere, water is precipitated in various ways and thus directly or indirectly affects animals. Dew is a most important water supply for some animals. Rain usually falls with little force, but clears dust from the air, modifies temperatures, and washes away soil. Hail may do actual injury to animals. Water vapor as clouds prevents radiant energy from reaching the earth. Enough water falls each year to make a uniform layer about 3 ft. in depth over the entire earth if it were allowed to remain evenly distributed everywhere. The seasonal and geographical distribution of water of precipitation exerts an important influence on climate and exercises more or less control over the types of vegetation

and animal life that may exist. Where a hot and dry season coincide, there is usually a steppe or desert formation; where moisture and heat come together there is forest. When precipitation is erratic, many plants and animals cannot become established where an evenly distributed water supply would otherwise permit them to live. Along the borders of the Sahara Desert birds are arranged in zones that are related directly to annual rainfall (Heim de Balsac 1935). Harper (1918) has pointed out that the productive agricultural districts in the United States are those where rainfall comes largely in early summer. Many cyclic activities of animals are initiated by seasonal rains, *e.g.*, the migration and spawning of many fishes and amphibians.

Humidity and Evaporation.—In terrestrial environments humidity exerts its most profound influence on animals by affecting evaporation of water from body fluids. The saturation deficit in air is therefore more significant than the absolute amount of water present. In the humid tropics, where air has little evaporating power, aquatic animals often wander over land. In arctic or alpine regions poikilothermic animals are largely or wholly aquatic. Cold air has little ability to hold moisture and when warmed soon attains high evaporating power. Air movements accelerate evaporation and drying. The rate at which water evaporates from a surface depends upon a variety of things, among which the character and extent of the surface, saturation deficit of water in surrounding air, temperature, and velocity of air currents are most significant. The evaporation from a surface does not depend only on saturation deficit of surrounding air but is also associated with "the difference in concentration of water molecules between the layer of air immediately in contact with the evaporating surface and the air above" (Leighly 1937). Vapor may pass into saturated air from boiling water; dew may form in unsaturated air. A gradient must be appropriately directed toward or away from a surface. Evaporation is determined more by energy on a water surface than by humidity above (McEwen 1930). In Ohio evaporation was found to be four times as rapid from porous cups in open pastures as from those in thick woods (Wilson & Savage 1936). Periodic fluctuations in humidity (daily, seasonal, etc.) profoundly influence the behavior of animals. Usually night air is cooler and more nearly saturated with moisture than day air.

Large homeothermic animals commonly evaporate water from their external or internal surfaces to cool their bodies, and suffer discomfort in high temperatures and humidities. At comparable temperatures small vital systems, such as insect eggs and larvae, develop more rapidly in high humidities (Knoche 1932, Mellanby 1933, etc.). However, an adult insect may lose more water in moist than in dry air, probably because it keeps its spiracles closed more in the latter (Mellanby 1932). However, adult insects often fly most during dry weather (Davies 1935), and pests may increase after such favorable periods (Eyer 1931). Death following water loss in such a small animal appears to be due to increase in concentration of body fluids and not to the exhaustion of nutritive materials (Buxton 1932, 1933). Most animals that live in the atmosphere have adaptations that enable them to impede or stop desiccation. Some have remarkable ability to lose water from their bodies and survive.

Probably no animal can live if it is completely desiccated, but many can exist for long periods of time in dry air. Even many marine animals when left exposed on beaches by low tides can stand the desiccating effects of air. Sea anemones have been kept for eight days in a laboratory without water. Though they come to look like dried raisins, there was apparently no particular injury, and the animals soon became active again when placed in sea water. Dragonfly nymphs have been kept in dry sand for 10 weeks and become active when water was added to the sand. Nematodes can be kept in a dry state for a quarter of a century without dying. The eggs of some aquatic animals (many crustaceans, rotifers, etc.) can stand long periods of desiccation, and some apparently will not hatch unless they have been dried for a time—which may extend to as much as 10 years. Hall (1922) tried the effects of keeping various animals in a dry chamber. He found that different types survived the loss of water as follows, the figures representing percentages of body weight: earthworm, 69.6; leech, 70.3; mealworm, 52.6; salamander, 47; frog, 41; turtle, 33.1; lizards, 33.8 to 47.8; mice, 24.2–32.1.

The length of time that animals can endure atmospheres of low relative humidity in general depends primarily upon the kind of integument and secondarily upon the proportion of the body surface to the body mass.

Hall kept horned toads, *Phrynosoma cornutum* Harlan, alive without food for nearly four months in a desiccator. Babcock (1912) kept larvae of the bee moth in a desiccator for 150 days.

Animals respond to the drying effects of the atmosphere in various ways. Usually the rate of metabolism becomes slower as an animal is dried. In many simpler animals secretions that aid in encystment are stimulated by drying. Encystment, estivation, or some other resting state is often induced by desiccation. Shelford (1914) studied the effects of the evaporating power of air on a variety of animals and found that the responses occurred whether evaporation was "produced by movement, dryness, or heat," that "the sign and degree of reaction" were correlated with the rate of evaporation in habitats from which the animals were collected, and that there was a general agreement between survival time and the character of the integument.

Many animals are very sensitive to changes in humidity, and numerous notes have been published concerning "weather prophets" among them. Shelford has suggested that such responses are induced by a disturbance of "neutrality" (in relation to acids and alkalies) in the body fluids by changed rates of evaporation. In the human body there is a high degree of cooperation between the skin, lungs, and kidneys, so that the amount and channels for water losses best suit the needs at any particular time. Loss of water through the skin cools the body most. That channel is usually used most during warm, and least during cold, weather.

Water in Organisms.—Water, according to Henderson (1917), has a significant circulation through living things: it serves as food; solvent; circulating medium; temperature regulator; and catalytic, hydrolytic, and ionizing agent. Water is a necessary constituent of all protoplasm and constitutes from 40 to over 90 per cent of the substance of living organisms. The amount present in an animal often has a marked influence on the animal's adaptability to other environmental factors. For example, many animals are able to endure wider ranges of temperature variation when they have a minimum of water in their bodies. With carbon dioxide water is built by plants into sugars and then into organic compounds which form the food basis for all animals. Water is essential for all "vital" phenomena; and, if a supply is not readily available, animals may

satisfy their needs by breaking up chemical compounds in their food to get it (Babcock 1912). It is necessary for circulation, nutrition, respiration, excretion and the regulation of temperature. Humidity as well as temperature commonly influences the metabolic rate of poikilothermic land animals. The state in which water occurs in animals may affect responses. After studying water in certain beetles Robinson (1928) concludes that those with least total water have the greatest percentage of bound water and that "the nature of response to external stimuli may be affected by specific colloids of a species." Mellanby (1936), investigating mealworms, bedbugs, clothes moths, and tsetse flies, concluded that metabolic rate as judged by food utilization was dependent on temperature and essentially independent of humidity in the surrounding air.

Water in Soil.—In soil, water is not only important as a solvent and transporting agent but in various ways makes soil habitats livable for plants and animals. Bouyoucos (1920) classifies the waters in soil as: (1) *gravitational*, which, of course, stands at the lowest level possible; (2) *free*, which is between the soil particles and freezes at −1.5°C.; (3) *capillary-adsorbed*, which freezes at −4°C.; and (4) *combined* water of solid solution or hydration, which does not freeze. The "wilting coefficient" of plants, which has been used by botanists as a measure of available soil moisture, appears to be "at the point where free moisture ends and capillary-adsorbed moisture begins." The availability of water in soil, therefore, depends not only on the amount present but upon the physical character of the soil itself. Many instances might be cited to demonstrate the importance of soil moisture for the activities of various animals. Earthworms come out on the surface of the ground when the soil is full of water, and when the soil dries they burrow, seek deeper levels, and finally roll up into balls. Certain species of tiger beetles will not lay their eggs except where the moisture content of the soil is within certain limits, and the larvae of these insects burrow deeper during dry seasons. Porous soil is favorable for insects because there is less likelihood of drowning during rains. The reaction of soil water is important, and poor drainage through the soil usually brings about stagnation and acidity. An unusual quantity of mineral salts in soil may make it "physiologically dry" because, though water may be abundant, organisms are not able to use it. As air

in its water relations is judged largely by its evaporating powers, so soil is judged by its water-supplying powers (Livingston 1935). The amount of water that may evaporate from soil surfaces is 20 to 90 per cent of that which may pass off from water surfaces of equal areas under the same conditions (McEwen 1930). Mulching soil by cultivation sacrifices water in surface layers to conserve that below. A light rain that wets only such a surface does not supply water to roots or soil animals (Briggs & Belz 1910).

Soils and Bottoms

Edaphic Factors.—Soils are of vast importance in their influence on the distribution of plants, and, as land plants are generally more important as food resources because they have better access to sources of energy that activate the production of organic substances and are therefore of more immediate interest than aquatic plants, plant ecologists commonly refer to "edaphic" (soil) factors as distinguished from climatic factors. Pedology has advanced rapidly during recent years, and many treatises on soil science have been published. In aquatic habitats various types of bottoms support characteristic societies of plants and animals, but organisms that live in such situations are usually less influenced by the substratum on or above which they exist because they are continually bathed in water, and many of them cannot live at great depths because they are dependent upon light from the surface. A terrestrial animal is dependent on soil to supply materials for food production. Many land animals use the surface of the soil as a base over which they carry on their activities, held to the outside of the earth by gravity; others take advantage of the stability that it offers as a habitat by burrowing about in it during all or certain phases of their life cycle. Soil is a stratified mixture of inorganic and organic materials.

Soil Formation.—Soil-making forces include oxidation, carbonation, hydration, solution, mechanical action of water and ice, temperature effects, wind, plants (especially bacteria and other fungi), and animals (Bowman 1911). The mineral crust of the earth is invaded by these forces and converted into soil. Many minerals when oxidized break up. Carbon dioxide also contributes to the weathering of rocks, frequently by converting silicates into carbonates. Water is probably the most potent

weathering agent in most soils through its solvent action. Solution is often associated with hydration or carbonation and thus contributes to chemical changes. Water also acts as a mechanical carrier. Nearly 5 billion tons of mineral matter is annually carried away in solution from land to sea, and the amount of sediment is many times greater. Water by freezing and thawing breaks up minerals and thus disintegrates them. Changing temperatures produce stresses in rocks and help to break them up. Winds not only move particles over the surface of the earth as dunes or drifts but also transport large quantities of fine suspended particles long distances. Bacteria that obtain part of their nourishment from the air may live in an essentially mineral environment and change it. They prepare rocks for utilization by other types of vegetation. Plants penetrate soils, help disintegrate them, and produce organic materials which enter into soils. Burrowing animals such as earthworms, millipedes, collembolans, and rodents mix soil, infiltrate it with their own products, make it more porous, and thus modify its water-holding capacity. Protozoans change the composition of soils by devouring bacteria. A mature soil becomes a complex system of living and nonliving materials—not inert but active. In order to emphasize the part played by living plants and animals in soil formation, Taylor (1930) proposed the following formula:

$$S = M(C + V + VA + A)^T + D$$

where A signifies animals; C, climate; D, erosion or deposition; M, parent material; S, soil; T, time; and V, vegetation.

Soil Constituents.—Soil consists of "(1) mineral matter, (2) organic matter, (3) soil moisture, and (4) soil air. The last two are, strictly speaking, dependent variables and in amount and character controlled by the mineral and organic matter. We may thus conceive of the soil as a three-phase system with an infinite number of components" (Robinson 1936). The three phases (solid, liquid, gas) are continually changing their relations but remain more or less in equilibrium. The solid constituents are classified by particle size (diameter) as follows: coarse sand 2.0–0.2, fine sand 0.2–0.02, silt 0.02–0.002, and clay < 0.002 mm. by the International Society of Soil Science. Fine soils usually contain considerable colloidal material and therefore shrink when dried. Organic matter usually does not exceed

10 per cent in amount, but in certain tropical soils it is below 1 per cent and in peat constitutes nearly all of the dry matter. Organic and inorganic colloids commonly occur together, often as coatings on inorganic particles. Soil solutes are commonly dissociated into ions. Soil air contains more carbon dioxide than the atmosphere above and somewhat less nitrogen and oxygen. It is more or less saturated with water vapor. The difference in the volume of constituents and the volume of soil that they make up is pore space, which generally varies between 40 and 60 per cent. Turning over soil, as by cultivation or the activities of burrowing animals, of course increases pore space and thus favors water movement and aeration. Change from crumb structure to single particles, packing, and other means that decrease pore space have opposite effects.

Soil Types.—Many classifications of soils have been published, and pedologists agree that such systems are as yet in a formative state. Lyon and Buckman (1929) present the following:

Sandy soils	Loamy soils	Clayey soils
Gravelly sands	Coarse sandy loams	Gravelly clays
Coarse sands	Medium sandy loams	Sandy clays
Medium sands	Fine sandy loams	Clays
Fine sands	Very fine sandy loams	Heavy clays
Very fine sands	Loams	
	Silty loams	
	Silty clay loams	
	Clay loams	

These pedologists define loam as "a soil possessing sandy and clayey properties in about equal proportions." Robinson (1936), "premising that the most fundamental distinction between soils depends on the character of the leaching process," states that well-recognized groups of soils may be classified as follows:

Soils with Complete Leaching—Pedalfers
- Acid Humus Present
  - Humus Podsols
  - Iron Podsols
- Acid Humus Absent
  - Temperate
    - Brown Earths

- Degraded Tshernosems
- Prairie Soils
- Sub-tropical and Tropical
  - Red Loams
  - Lateritic Soils
  - Laterites
- Soils with Incomplete Leaching—Pedocals
  - Tshernosems
  - Chestnut Earths
  - Brown Desert Soils
  - Gray Desert Soils
- Soils with Impeded Leaching—Hydromorphous Soils
  - Absence of Soluble Salts
    - Sub-arctic
      - Tundra
    - Cool-temperate
      - Meadow Soils
      - Gley Podsols
      - Peat Podsols
      - Peat Soils
    - Sub-tropical and Tropical
      - Vlei Soils
  - Presence of Soluble Salts
    - Saline Soils
    - Alakaline Soils
    - Soloti Soils

Podsols in the Northern Hemisphere occupy the humid regions south of the tundra. They are usually developed under coniferous forest or heath. Brown earths are usually developed under deciduous forest and have been subject to a little less leaching than have podsols. Degraded tshernosems are the gray forest soils of Europe, perhaps developed in former steppes. Tshernosems are "black earths," with considerable organic matter. They are base-saturated. Chestnut earths contain less organic matter; brown and gray desert soils, still less. Tundra occurs in subarctic regions where the soil is full of water; a deep frozen stratum is characteristic. Gley and peaty podsols are also water-saturated. Vlei soils occur in certain African basins where there is seasonal wetness. Soloti soils are degraded alkaline soils in which there is a bleached eluviated upper stratum rich in silica because alkalies have leached out.

Soil Profiles.—Every developed soil shows more or less stratification. The strata are usually called *A*, *B*, and *C* horizons, and these may be subdivided. As soil is formed it always tends to develop characteristic layers which may be exposed by digging a trench. The complete succession of horizons down to undifferentiated parent material is called the "soil profile." It results largely from movements of water in soil, which leach or raise soluble materials. In eluviation, water may move materials mechanically or chemically. Materials also may be illuviated or transported into a different stratum. Figures 15 and



	CHARACTER	STRUCTURE
	VEGETATION	
A_0	FIBROUS LAYER	
A_1	AMORPHOUS PEATY LAYER	
A_2	ASHEN-GREY OR LIGHT GREY, LAYER, LEACHED OF HUMUS AND SESQUIOXIDES, BLEACHED SAND GRAINS, STONES, AND GRAVEL	LOOSE STRUCTURE WITH ELUVIATION OF CLAY
B_1	BLACK TO DARK BROWN LAYER OF HUMUS ACCUMULATION. BLACK STAINING ON STONES AND GRAVEL	COMPACT STRUCTURE WITH ILLUVIATION OF CLAY GREATEST COMPACTION IN B_1 LAYER
B_2	BROWN TO ORANGE-BROWN LAYER OF SESQUIOXIDE ACCUMULATION. BROWN IRON STAINING ON STONES AND GRAVEL.	
C	GRAY OR BROWNISH-GRAY PARENT MATERIAL	

FIG. 15.—Diagrammatic representation of a typical podsol profile. (*After Robinson* 1936.)

16 show a typical podsol profile and those of cultivated and virgin forest soils.

Soils as Habitats for Animals.—Soil is used by various animals as a refuge from enemies, to escape desiccation and extremes of temperature; as material for abodes; and as a highway. Clay is cold, dense, poorly aerated, and, though it holds much water, does not give up water readily to plants or animals. Sand is dry and loose (caves in readily) and has a variable temperature. Rock heats and cools quickly, has little available water and practically no air, and is usually too resistant to allow penetration by burrowing animals. Alkaline soils are "physiologically dry" because the salts present hold the water so that it is not

readily available to organisms. Humus has a great water capacity and gives up water readily, is usually well aerated, and furnishes nitrogen as well as mineral salts and water. Peaty soils and raw humus are uninhabitable for most animals because they are poorly aerated and have an acid reaction. If a porous soil rests on an impervious substratum, the slope is important. If

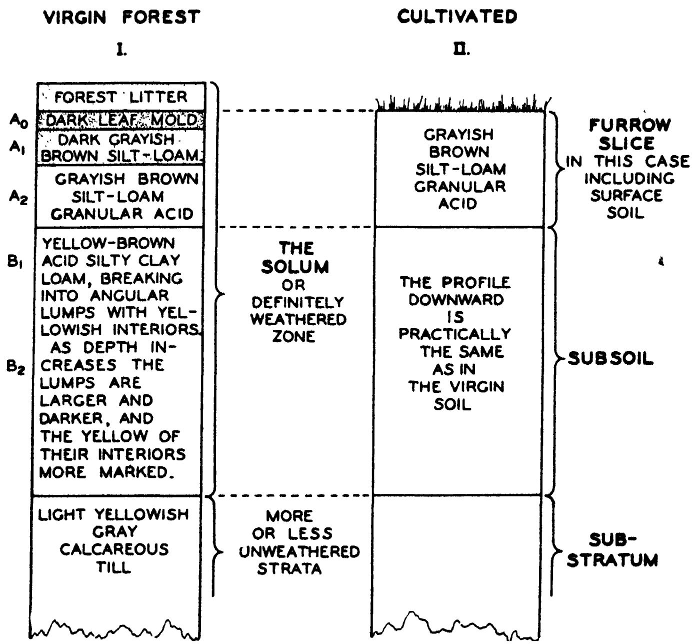


FIG. 16.—Profile diagram of virgin forest and cultivated field derived from the same parent materials. (*After Baldwin* 1927.)

there is a depression, water does not run off and collects—thus forming a swamp or wet meadow. If both topsoil and subsoil are readily penetrated by water, conditions may be too dry for animals. In general, the character of the vegetation cover serves as a good index of the habitability of soil for animals; conditions that make plants flourish are usually favorable for animals.

Soil Water.—Water in soil affects animals in various ways. A wet soil usually contains very little oxygen and may be "sour" on account of putrefaction. Winter and spring are bad seasons for subterranean insects because water forces the air out of the soil. In dry soils the height of the water table controls the

available moisture to a considerable extent. Above the standing water, animals depend on percolation and the ability of the soil itself to "raise" water. The total amount of water present is not so significant as the amount that is available for the use of animals. A soil is physiologically dry if an organism cannot extract water from it. Soil dries through the evaporation of its water and on account of the consumption of water by organisms in it. The rate of loss by evaporation depends on the saturation deficit of the atmosphere, slope, and exposure. Other factors being equal, dark-colored soils dry most rapidly. The seasonal distribution of soil moisture is important. The most productive agricultural regions in the United States are in areas where rains occur in spring and early summer; in regions where rains come in later summer, land is not so valuable.

Soil Temperatures.—Soil is warmed by the sun and by the decomposition of organisms in it. Most soil animals are adapted so that dry cold does them no particular harm. Some burrowing animals, like the earthworm, have a very wide range of toleration for temperatures; others, like the mole, are stenothermic. In the temperate regions of the earth there is a vernal and autumnal "overturn" when the thermal relations between shallow and deep soils change. Where there is no snow, the average temperature of soil is higher than that of the atmosphere above it; where snow falls, soil temperatures vary. Daily fluctuations in temperature extend to a depth of about 1 m. Annual fluctuations may reach down to 25 m. In England the differences between depths of 8 and 67 cm. vary from 2–4.5°C. at different seasons. In Michigan the average annual range for two years has recently been determined as follows: at 1 ft. 27.8°C., 2 ft. 21.4°C., 3 ft. 15.7°C.

Soil Cover and Its Effects.—The living and nonliving covers for soil have a marked influence on its characteristics as a habitat. Snow, dead leaves, and grass conserve moisture and serve as a blanket to prevent rapid thermal changes. Each species of plant does best in certain degrees of alkalinity and of electrolytic dissociation. Many plants are able to change the soil to some extent, so that it better fulfills their requirements, *i.e.*, they change the substrate into that in which they flourish best. Calcium is apparently necessary for plants, not only for its own peculiar qualities but as a catalytic agent in the assimilation

of other mineral substances. It is also a necessary constituent of soil for certain animals, *e.g.*, land snails do best in limestone regions. In bogs, soil acidity increases at greater depths, but in drier soils it usually decreases.

Organisms in Soil.—In one locality the bacteria in raw humus have been estimated to number 22,000 per cubic centimeter; in rich soil, over 2,500,000. Lohnis and Fred (1923) say:

> Not infrequently a hundred million are found in 1 gram of soil, where they nearly always exert the greatest activity . . . One acre contains, therefore, about 350 pounds of living bacteria besides 175 to 350 pounds of fungi, protozoa, and algae, altogether 525 to 700 pounds per acre.

Waksman (1924) has shown that the hyphae of fungi are usually abundant when soil is acid and decrease when fertilizers that make the soil less acid are added. Protozoa in soils appear to feed largely on bacteria and are an important factor in decreasing them. There may be thousands of nematodes in the upper foot of an acre of fertile soil. Insects are most abundant in a stratum from the surface to about 10 cm. below but often burrow deeper to pupate or hibernate. The distribution and the activity of earthworms are largely influenced by moisture. Burrowing animals help to form, renovate, and maintain soils. Branner (1912) studied ants and termites in Brazil. He found that their excavations aggregated several miles per acre. They affected the soil by admitting air and rain through their burrows, bringing dirt to the surface, carrying down organic matter, and producing substances that attacked the soil and broke it up. In an area near small ponds in the Indiana sand dunes Sanders and Shelford (1922) found about 100,000 burrowing and surface animals per acre (250,000 per hectare). Important among these were tiger beetles and their larvae and digger wasps, with smaller numbers of ground beetles and white grubs. A considerable part of the surface fauna consisted of adult insects which came from neighboring aquatic habitats.

Types of Bottoms.—In marine and lacustrine habitats the character of the bottom is determined largely by the movement of water. Rocks are characteristic of exposed, wave-beaten shores; sand is found in turbulent bays; mud and ooze typify quiet water. Although the same is true to some extent in streams,

the bottom also reflects the nature of the soil traversed in each drainage system. Rock and sand are generally not so productive of animal life as mud, but some rocky sea beaches have a very abundant fauna. Mud bottoms usually have the advantage of an abundance of food, both from mineral sediments and from the organic remains of plants and animals, but have poor aeration. Plants often flourish and alleviate stagnation in such places by using up carbon dioxide and producing oxygen. Mud dwellers often have special means for respiration. They come to the surface for air, possess hemoglobin for carrying oxygen, or have other peculiarities.

Animals Associated with Various Bottoms.—It is well known that certain species of fishes, worms, molluscs, and other animals are associated with particular bottoms. Pond (1905) maintains that aquatic plants draw nourishment in through their root hairs and require certain compounds for growth. There is selection of habitat by animals on the basis of bottom material. In his study of the molluscs of Oneida Lake, Baker (1918) found the number of species indicated on each type of bottom: mud, 50; sand, 42; clay, 35; gravel, 33; boulder, 27; sandy clay, 25. The living organisms on or in a bottom may change its character by causing sedimentary deposits, precipitating substances from the water, and in other ways. Calcium carbonate is often deposited by green plants. Mangroves, eelgrass, and the biota associated with such plants cause characteristic accumulations. Quicksands often engulf and smother animals. They occur only where water flows upward through finely divided material.

MOVEMENTS IN MEDIA

Molar Agents.—In speaking of molar agents Davenport (1908) said:

> The subject is so ill-defined that it is impossible to draw any line of distinction between contact on the one hand and a crushing pressure, or wounding, on the other. The molar agents may be solid or fluid. The methods of application may vary from a blunt contact or a sharp cut or puncture to the impact of a flowing liquid. All these agents have this in common, however, that they act in a gross, mechanical way.

Molar agents are important as makers of habitats. Running water carries earth and even wears rock away (Fig. 17). Rain

and river erosion are familiar aspects of physiography. Ice also pushes up ridges, scours out valleys, cracks up rocks, and works in other ways. Wind moves sand dunes, dries soil, transports floating objects and leaves them along drift lines, and may break down vegetation. The wind also brings about the ceaseless pounding of water waves, which are so important in many habitats. Tides and other movements in water cause currents that pick up, carry, and deposit sediment and in other ways markedly affect the activities of animals. Currents and waves in water

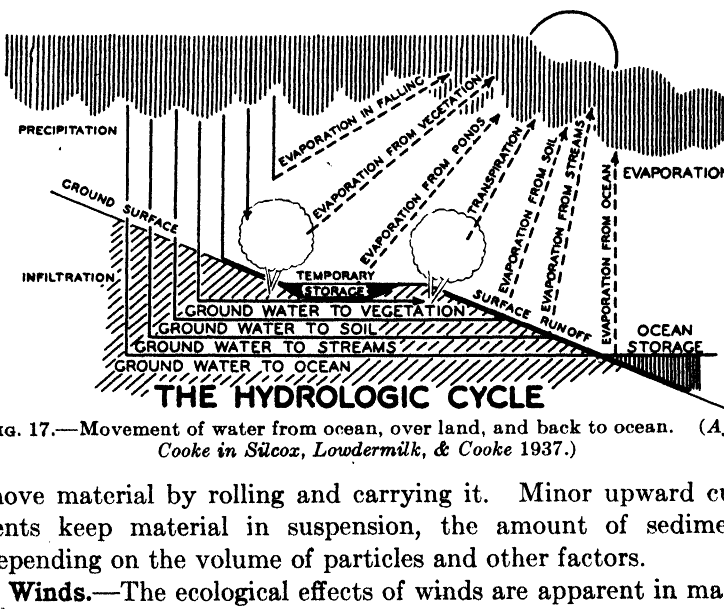


FIG. 17.—Movement of water from ocean, over land, and back to ocean. (*After Cooke in Silcox, Lowdermilk, & Cooke* 1937.)

move material by rolling and carrying it. Minor upward currents keep material in suspension, the amount of sediment depending on the volume of particles and other factors.

Winds.—The ecological effects of winds are apparent in many habitats. The most important physiological influences of moving air are perhaps due to its drying and temperature-changing qualities, but air movements in themselves are important. Migrations are helped and hindered by winds; floating objects bearing animals are blown across oceans, and animals are carried across deserts. Scale insects and the gypsy moths are known to spread with the wind. The cotton boll weevil traveled north through the United States most rapidly during windy years. Aphids have been seen to tumble off the tops of plants into strong winds. Mosquitoes and flies, which usually do not travel more than a mile or two, may be blown many miles by hurricanes. Honeybees are often lost during storms. Winds blow many land

animals into the water, where they are drowned. Certain insects and birds on oceanic islands largely escape such danger because they are wingless. Winds help many animals find food or mates and may give notice of the presence of enemies by carrying odorous substances. Most flying animals depend on air currents to a considerable degree as a means of locomotion—not that flyers are necessarily carried with the wind, but air in motion enables animals moving through it to overcome gravity more readily. Wind often limits the local distribution of animals, particularly in exposed situations where they may be confined to hollows or other sheltered places. Wind benefits certain habitats by removing injurious gases and by disseminating the minerals, carbon dioxide, pollen, and seeds that are so necessary for the maintenance of plants, which, in turn, always furnish the ultimate food resources for animals.

Currents.—Currents in water are largely due to winds, the rotation of the earth, and differences in pressure due to variations in level. Their direction is often influenced by the contours of containing basins and the positions of outlets. Currents in the ocean are not sharply defined and rarely run along as "rivers" but appear at the margins of great eddies (Fig. 18). They serve to distribute, select, and annihilate myriads of animals. They may be permanent, seasonal, or adventitious. In a general way ocean water moves toward the poles at the surface and toward the equator in deep water; but winds, shorelines, and many other factors influence its movements. Currents that are induced by winds tend to flow in parallel lanes with transverse or oblique currents between them (Langmuir 1938). These indicate the direction and extent of helical vortices, which may extend to considerable depths. The abundance of animals on certain parts of the ocean bottom is due to currents; for where two different types of water meet, many organisms are continually dying, and these furnish abundant food as they sink. The growth form of individual animals and of great aggregations, like oyster beds and coral reefs, is often dependent on currents. In freshwater, currents not only distribute food but are important in the oxygen supply of many animals. In streams and lakes the amount of dissolved oxygen is frequently correlated with the rate of flow. Stream and pond isopods react to currents according to the amount of oxygen present in the water that surrounds them

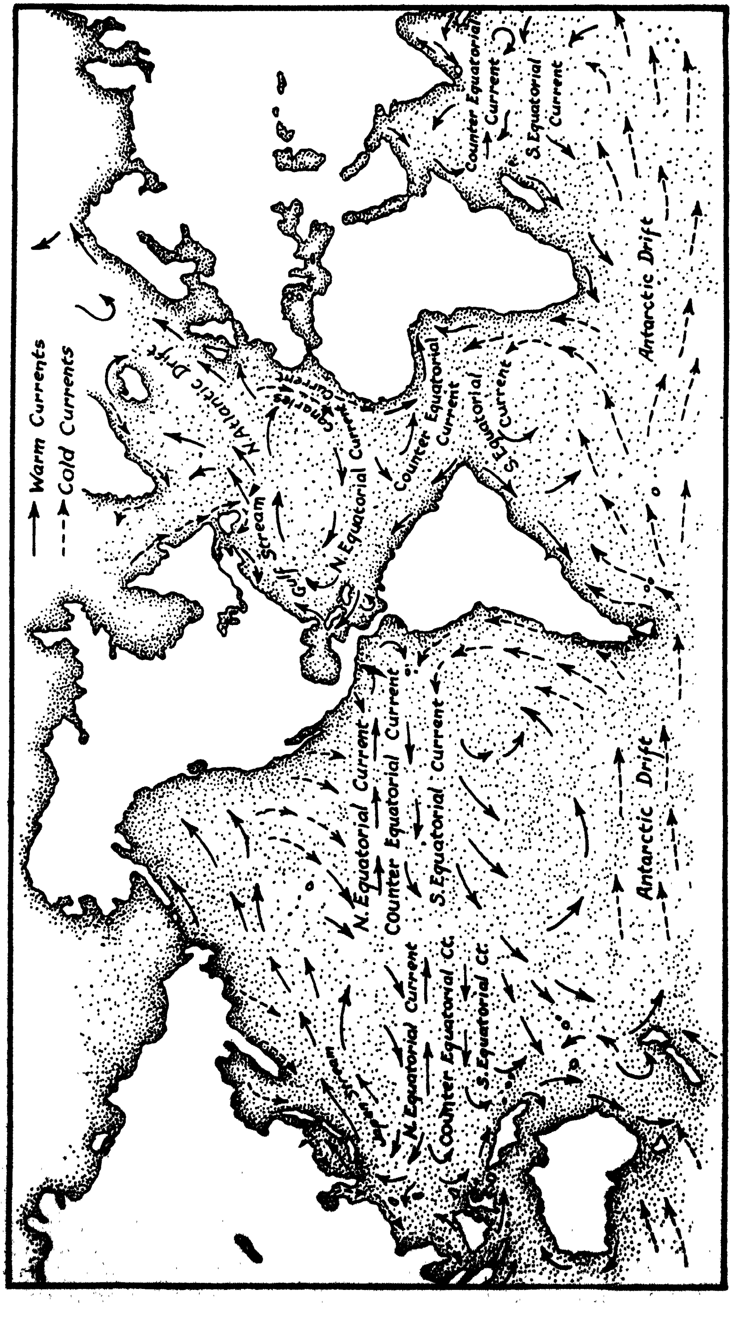


Fig. 18.—Surface currents of oceans. (*After Borradaile* 1923.)

(Allee 1912). Shallow lakes in which there is vertical circulation at all times are quite different habitats from deep lakes in which the deeper water stagnates through all or part of the year. In rivers the most abundant bottom fauna is usually found where the current is most sluggish (*i.e.*, on mud), and currents above a moderate speed appear to limit the quantity of plankton that may develop. The species of fishes in streams are arranged roughly in a graded series from headwaters to mouth according to the swiftness of the current. The larvae of caddis-flies are also arranged according to the swiftness of the water, different types of cases being apparently adapted to different strengths of current. The areas of the gills of May-fly nymphs are correlated with the swiftness and oxygen content of streams.

Waves.—Waves in water are due to currents, winds, or the combined effects of both. There may also be waves in loose sand or snow when moving air can pick up, carry, and drop particles. Surface waves in water generate a series of trichoidal circles which grow smaller with increasing depth. In great storms the effects of surface waves may extend down as much as 600 feet, which is about the depth of continental land shelves. Waves on beaches tend to move stones and other large objects up toward high-water mark and to move sand back and forth according to their direction. Sand settles about 2 in. per second, and it cannot be carried by water that has an upward movement of less than 2 in. per second (Cornish 1910). In lakes, exposed shores usually have a scantier population than protected bays; and, to a lesser degree, the same is true in the ocean. There are some marine animals, however, like acorn barnacles, that flourish on rocks that extend into the open ocean, where they receive the full force of the waves and, of course, have opportunity to capture much food from the water.

Tides.—The ocean tides cause a rhythmical succession of currents in littoral habitats (Fig. 19). Many animals are adjusted to this rhythm. Podurans migrate up the beach and burrow to a depth of 6 to 8 in. when the tide comes in and emerge in great numbers when the tide ebbs. In clams there is a rhythmical formation and destruction of the crystalline style which is correlated with the ebb and flow of the tides. Nelson (1921) found that oysters fed over 20 hours each day and that 73 per cent of the shell closures were at ebb or very low tide. It has been

stated that the periwinkle, *Littorina litorea,* shows a vertical migration which is synchronous with ocean tides and that such migrations take place regularly when the snail is placed in an aquarium where there is no tidal action. Haseman (1911) has shown, however, that this snail is stimulated to move up and down by the surface film as the water rises and falls and that in the absence of tides no rhythmical migrations occur.

Adjustments of Animals to Molar Agents.—The adaptations of animals to waves and to strong currents are similar. Many animals that live in moving water are sedentary or fixed.

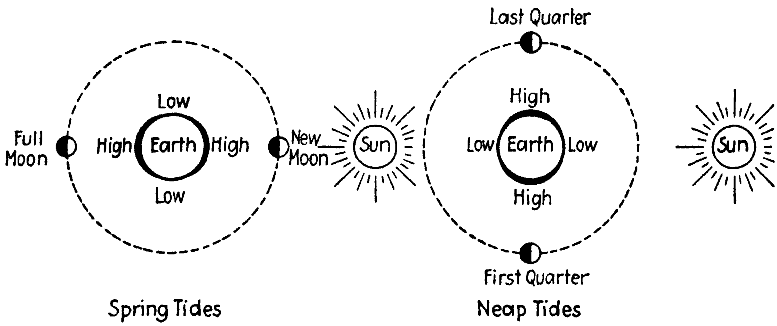


Fig. 19.—Showing the relation of the sun and moon to spring and neap tides.

Onchidium, a pulmonate snail in Bermuda, lives in crevices in rocks and comes out for a little time each day when the tide is out. Some animals have flattened bodies and have developed organs for adhesion, such as suckers, clinging hooks, and mucous or cement glands. Others have strong shells which cover the body (clams, snails, barnacles). The horny layer on the outside of many mollusc shells protects them from abrasives. Animals that live on shifting sand bottoms are usually burrowers or good swimmers. Many of the animals in moving water depend for food on adhering algae or the floating life in the water itself. In rapids, caddis-fly larvae spread delicate nets which they scrape off at intervals for food. Slender-legged spiders run over the surface and catch struggling insects, if trout do not pick them off from below before they arrive. On the ocean beaches, snails continually rasp algae off the rocks; clams siphon water through themselves and strain food from it; bryozoans and barnacles spread their nets and catch what they can. Along lake beaches, crayfishes lurk among the rocks; waterpennies, May-fly nymphs,

and leeches hide beneath stones. Some net-fishing crustaceans have taken up their abodes inside the shells of molluscs and in worm tubes, where strong currents bring them food.

Stagnation.—Semper (1881), in his classical chapters on "the influence of stagnant water" and "the influence of a still atmosphere," has carefully considered the adaptations of animals that live in the absence of molar agents. Stagnation is associated with adaptations in organs of respiration, and many aquatic animals that live in quiet water have means for acquiring oxygen from the atmosphere. Some animals when they grow in quiet water show different forms from those that they assume on wave-beaten rocks. Certain sponges and corals growing in lagoons or deep water may assume a branched or spreading form, and the same species on exposed beaches are flat or encrusting. Some animals die very quickly if water becomes stagnant; others can stand prolonged submergence in it. Fulton (1921) kept a Bermuda anemone sealed up in 100 cc. of water for 6 days without apparent injury.

Earthquakes.—Profound earth movements of course greatly affect animals, particularly along the shores of seas. When beaches are uplifted, littoral animals die of starvation and exposure in air. When they sink, terrestrial animals are drowned. Great earthquakes are often accompanied by tidal waves which do great damage as they sweep over shores. Incidental fires, the breaking of oil tanks, and other sources produce toxic substances which poison aquatic and terrestrial animals. After the great earthquake in Japan in 1923 important food resources in littoral waters were greatly depleted or destroyed (Kaburaki 1926) when certain beaches in Sagami Bay rose 1.4 m. It required several years for algae, snails, worms, crustaceans, clams, and other littoral organisms to repopulate the shores. Many fishes and other neritic animals also were killed in great numbers. Above the water there was at first a stinking zone of dead littoral animals and plants, later a crumbling waste of dead shells and other debris.

BIOLOGICAL FACTORS

Biotic Factors.—In the foregoing discussion of factors, physical phenomena in environment have been considered. Attention is now given to living plants and animals as factors in environment.

There are two aspects of this subject: (1) each species, indeed even each individual, has inherent qualities that make it fit a particular environment and also make it exert peculiar and characteristic influence on its surroundings; and (2) plants and animals as individuals, or as more or less complex societies, give environment certain qualities that make it favorable or unfavorable as a habitat for other types of organisms. For example, a polar bear has certain anatomical and physiological characteristics that make it at home in icy oceans. Its presence in the arctic and its absence in the antarctic give the faunas of the earth's two polar regions quite different aspects. Flightless penguins flourish in the antarctic ocean; but if they were to be introduced into the arctic region, bears would probably destroy them very soon. The sea leopard often devours them in the water, but, by marching inland to breed in secluded rookeries, they are able to rear young and maintain their race. Biotic factors may be divided into (1) those concerned with extraorganismal relations, *i.e.*, those which result from the presence of plants or animals other than the one under consideration in an environment; and (2) intraorganismal relations, or those which are due to inherent anatomical or physiological qualities in organisms in an environment.

Extraorganismal Biotic Relations

Plants.—The characteristics of plants as organisms are mentioned in Chapter III, and the ecological importance of plants will be considered fully in Chapters V, VII, and XI. Here it is necessary only to indicate briefly the role of plants as factors in environmental complexes. Plants are of prime importance to animals as the ultimate source of foods, manufactured by photosynthesis and other autotrophic processes. Many of the large geographic areas of the earth are commonly named for the dominant plant types, as prairie, coniferous forest, deciduous forest. Plants as the food for vegetarian plants and animals thus limit distribution. On land and in water, plants not only furnish food but serve as shelters for other plants and for animals, giving protection from supraoptimum radiation, excessive evaporation, predaceous enemies, etc. Vegetation cover over soil conserves moisture and inhibits floods. It also tends to prevent extreme variations in temperature. Plants in water often help to supply

oxygen for respiratory processes, especially during warm seasons, when water can hold less gas in solution but photosynthetic processes are more rapid. The relations between plants and animals are considered in more detail in Chapter XI.

Animals.—Species living in the same area may have no relations with each other or be more or less intimately associated as predator and prey, commensal, symbiont, or host and parasite. In every region there must be a balance between producers and consumers. When an association has reached a steady state, populations remain fairly constant, except for fluctuations brought about by unusual variations in seasonal cycles, epidemics of diseases, and other varying factors that disturb ecological balances. There must always be enough vegetation to feed herbivorous animals without being exterminated; in turn, herbivores must be present in sufficient numbers to feed carnivores and yet survive. Competition and populations are considered in Chapter VII; rhythmic fluctuations in environment, in Chapter VI.

MORPHOLOGY

Forms of Animals.—The forms of animals are adapted, often to a striking degree, to the habitats in which they live. The ancestral pattern of structure that an animal inherits fixes its habitat in a general way, and animals that are not of close genetic relationship often show convergent similarity in their structural adjustments when they live in the same habitat. McClendon (1918) noted that Alpheus and Typton, two crustaceans that live in the canals of sponges, are very similar in form and coloration and cited this as a remarkable case of convergence associated with a peculiar habitat. From an evolutionary point of view it is not permissible to say that peculiar environmental complexes cause animals to assume particular structural adaptations, but the ecologist recognizes many peculiarities of structure that enable him to say with some assurance in which habitats the animals possessing them belong. Fishes from various systematic groups have a ribbon-like form which permits progress by lateral undulations of the body (in the more specialized fishes of this type dorsoventral flexure is not possible), and these are associated with quiet water where they lurk among crevices in rocks or vegetation and burrow in mud. Freshwater mussels show a

tendency to greater obesity as one leaves the headwaters of a stream and goes into the waters below. Many investigators have shown that the forms of plankton animals vary according to the condition of the water in which they live, and some species by their structure even indicate the locality and the season of the year at which they were collected. By the direction of the hair on the dried skin of a mammal, a naturalist can form an opinion of the postures, resting positions, and habits of the animal when alive. Animals show unending structural adaptations for nourishment, respiration, excretion, movement, reproduction, protection, and distribution. These are properly read by those who understand as signs of habits and habitats. Homology faithfully serves the taxonomist and evolutionist; scientific, critical analogy is a valuable aid for the ecologist.

Surface-mass Relations.—Probably the primitive form for simple animals was a sphere, and this has many disadvantages (Ryder 1886). As a body of living matter increases in size the materials on the interior are left far from surface membranes, and therefore there may be difficulties in carrying on nutrition, respiration, excretion, and other vital activities. When a cell grows to a certain size it must decrease its metabolic rate or divide and thus increase its working surfaces. In the past as the masses of animals increased, various expedients were evolved for keeping external surfaces near internal working tissues. Flatworms accomplished this end by spreading out into thin disks; roundworms became slender cylinders. Some animals spread cells outside a central cavity or mass of metabolically inactive jelly. Others increased surfaces within their bodies by having tubes or vacuoles inside their substance. Internal tubes were connected directly (sponges, insects) or through osmotically active membranes (annelids, branchiate arthropods, chordates) with the exterior. Surfaces for absorption or excretion were increased by coiling, folding, or the erection of lamellae or villus-like protuberances. A small animal can absorb and excrete simply and easily. A large one must possess more or less elaborate adaptations for keeping its internal parts fit.

Symmetry and Environment.—Child (1915) has attempted to determine the causes of the forms assumed by animals, and he has shown that they are associated with gradients in metabolism along axes. If there is only one principal gradient, the parts of

an animal are arranged in a lineal series, and the end of the chief axis that has the most rapid metabolic rate is the anterior end. If there are gradients along several axes, the animal is radially symmetrical. Child frankly states his opinion that the stimulus that determines the direction of the first gradient in an animal must come from the environment—perhaps at the point of entrance of a spermatozoon into an egg, from the point of attachment of an egg in an ovary, or from some other early determining influence. From an ecological point of view, however, environment plays a small part in determining the forms of most animals; heredity is the chief molder.

Perhaps the most apparent relation between structure and environment is in the fact that most animals that live attached or lead a sedentary life show a tendency toward radial symmetry, whereas those that move about are, as a rule, bilaterally symmetrical. It is apparent that some animals, like barnacles, that are now essentially radial in their symmetry, so far as their relations with the outside world are concerned, have been derived during their evolution from bilaterally symmetrical ancestors. On the other hand, some animals, like the spatangoids, that apparently come from radially symmetrical ancestors have a bilaterality superimposed on their primitively radial plan and at present move freely about. There are many instances where a change from an active free-living life to a sedentary one has been associated with a tendency toward radial symmetry, and many where a change from sessile to active life has been associated with the taking on of more or less bilaterality.

Variation in Structural Adaptations.—If structure kept constant pace with every change in habitat, there would be no stability and no species. But adjustment does not go so far as that. Most animals are able to make temporary minor adjustments, as in the case of calluses on carpenters' hands and variations in the lengths of Daphnia crests, but heredity apparently does not permit any fundamental permanent change in response to stimuli received from the environment. In some cases different species show gradations in structure in relation to variations in habitat, but on the whole such cases are rather rare. Dodds and Hisaw (1924) have recently accumulated some data in relation to the area of the gills on the May-fly nymphs of alpine streams and find that there is a rather definite relation between

area and swiftness of current—the swiftest current being associated with the least area. Rhode (1912), on the other hand, collected larvae of the flies of the genus Pelopia from a great variety of habitats and found that they were essentially alike in structure; but when he bred out adults from the larvae he found that various species were more or less segregated in different habitats. Some sessile marine animals (sponges, corals, etc.) show forms that are correlated with the turbulence of the water —being flat and encrusting on wave-beaten shores and growing into branching, treelike forms in quiet water.

Uses of Various Types of Structure.—Multicellularity, the presence of tissues, antimerism, metamerism, and colonial life give animals certain advantages in their relations with environment by allowing injury without incapacitating all units of the body system and by permitting division of labor. Chetverikov (1920) compares the plans of structure in insects and vertebrates, pointing out that, according to the principles of mechanics, it is to be expected that vertebrates, with endoskeletons and masses of muscles on the outside of the body, would be big, slow, and comparatively awkward, whereas insects, with exoskeletons and enclosed muscles, are at their best as small, active animals. Kennedy (1920) and Wheeler (1927) have carried such discussion much farther and admirably consider the profound correlation between habits and habitats in relation to external and internal structures of insects. Kennedy (1927*a*) points out that the presence of an exoskeleton makes insects small in size; sensitive to variations in temperature, moisture, light, and chemicals, and comparatively insensitive to sounds and touch stimuli; protects them against enemies of their own size and injury from falling; permits quickness, aerial life, and invasion of many habitats; conserves water; limits the volume of nervous tissues and thus makes behavior tropistic rather than intelligent; makes length of life short because little reserve tissue is available; and exerts other profound influences. An exoskeleton is three times as strong as an endoskeleton but condemns an animal to be small, quick, and unintelligent; whereas an endoskeleton, though tending to produce animals that are large and slow, is usually associated with greater reasoning powers.

Size of Animals.—Environment limits the size of animals in various ways. The size of snails confined in small containers

show direct relation to the amount of water surrounding them. Colton (1908) has shown that under such conditions dwarfing in *Limnaea columella* is due chiefly to limitations in food and oxygen and to the presence of excretory products. Abyssal animals often grow to very large size, and Solokowsky (1910) has advanced the view that this is possible because the perfect quiet at the bottom of the ocean enables them to spread out without risk of injury. Gravity is, of course, an important factor in limiting the size that animals may attain (Tirelli 1932, Dannevig 1933). In aquatic habitats soft animals such as jellyfishes and ctenophores are able to swim about because the buoyancy of water sustains them, but in air, animals must have sturdy skeletons to keep them from collapsing and permit locomotion. Only gastropods, arthropods, and chordates have attained land life. Of course changes take place when animals are able to leave water for land. For example, land snails have developed extensive mucous glands in their skin. These help to prevent desiccation and aid in creeping (Mazek-Fialla 1933).

Numerical Variations in Parts of Animals.—Environment may also influence the parts of animals numerically. The number of vertebrae in certain species of fishes varies more or less regularly with variations in seasonal temperatures, altitude, and latitude. Again and again in the past animals have multiplied parts (polymeres) to insure safety from injury and later in their evolution lost some of them and specialized others (anisomeres) to carry on particular functions (Gregory 1933). The toes of tetrapods came from lobe fins; the three pairs of legs on an insect are remnants of a long metameteric series. Zeleny (1923) has been able to control the number of facets in the eye of Drosophila by varying the temperature at which the flies were reared and finds that a logarithmic constant expresses the relation between the germinal and environmental factors. Bar-eye may mutate to normal eye (Morgan 1923) and thus produce a radical change in the perceptive abilities of the fly on which it occurs.

PHYSIOLOGY

Adjustment.—The reactiveness of organisms enables them to make adjustments to the environment. Animals show many adaptive physiological responses, the majority of functional changes being beneficial. There are continual adjustments to

temperature, salinity, poisons, and other variable factors in the environment. The chemistry of protoplasm is extremely complex and not as yet thoroughly understood, but doubtless chemical differences will be found to be concerned with such subtle differences in susceptibility as animals show to disease and infection by parasites and in ability to utilize various substances for food. Some animals are able to reduce greatly their total amount of metabolism when living conditions become unfavorable. The sea cucumber, *Thyone briareus*, when in stagnant water throws out most of its visceral organs (including the greater part of the enteric, nervous, and circulatory systems) and regenerates these when the surroundings again become favorable.

Types of Adjustment to Environment.—Reference has been made in another connection to the paper by Pike and Scott (1915) which points out that animals have three general types of adjustment to environment: (1) Those animals that live in an essentially unvarying environment—the ocean—have little need for adjustment and make little; (2) those that live in a variable environment—land or freshwater—may vary with it more or less and often have remarkable powers of adjustment; and (3) those that are to some extent independent of environment because they make adjustments that keep their internal conditions constant. In all the habitats of the earth it is essential that animals function properly; and if the environment varies so that they are not able to do so, it is "unsuitable" for them. Living things must function, for a certain amount of chemical activity is one of the primary characteristics of protoplasm. Physiology is the keystone of ecology. Plants usually show the effects of their physiological condition by their growth form to a greater extent than animals do, and they therefore often serve well as indicators of the conditions of environment. Each animal has a particularly inherited behavior pattern which it shows in its responses to environmental changes (Child 1924). As an individual it represents the more or less permanent results of physiological processes. It has some capacity for regulation. It has its pattern arranged according to one of three types: radial, polar, or bilateral. An animal operates through two correlative factors: (1) chemical-transportive and (2) excitation-transmission. There is physiological dominance of regions of high metabolic activity over those of lower activity, a gradient in physiological state.

Child believes that physiological gradients are the bases of patterns, which are of external origin. Animals survive and attain some degree of success in varying environments by adjustments. Susceptibility to injurious substances depends on rate of oxidative metabolism, especially in youth (Child 1923). Aquatic animals are able to tolerate wide ranges of ionization in the medium in which they live (Powers 1930) but may be quite susceptible to minute quantities of dissolved poisons. At different temperatures susceptibility may change radically without direct relation to the increase in metabolic rate which is usually associated with higher temperatures in poikilothermic animals. Such "critical thermal increments" (Crozier 1924) are often connected with the optimum ranges of activity of particular catalysts. In homeothermic animals there are many specific adaptations for keeping bodily conditions stable. Elephants' ears act as thermoregulators and are larger in warmer climates (Hesse 1928). A young wren after hatching is at first somewhat poikilothermic but becomes homeothermic as (1) its mass in relation to its surface increases, (2) insulating feathers cover its body, (3) its internal dissipating surfaces come under effective nervous control, and (4) its means for the production of metabolic heat become more efficient (Kendeigh & Baldwin 1928). A living individual is a harmonious whole of correlated, interrelated chemical differentials (Loeb 1936). There are countless types of adjustment.

Metabolism.—Davenport (1908) says that "metabolism is life" and points out that it is limited by two sorts of conditions: (1) structural, such as broken parts or changed chemical compounds; and (2) dynamic, such as absence of light, water, and proper temperature. In adjusting itself to environment an animal must acquire food to maintain metabolism and convert foodstuffs into assimilable substances. In such processes bacteria are often important aids, particularly in the digestion of cellulose. The bacterial flora in the digestive tracts of carnivorous and herbivorous animals is radically different, anaerobic putrefactive forms being abundant in the former and not in the latter. Metabolic processes furnish energy for the accomplishment of the work necessary for normal activities. The chief source of energy is from oxidation, and one of the important relations of animals with environment is the securing of a continual supply

of oxygen. There must also be opportunity in the environment for the disposal of waste products. Living things are continually producing acids, and buffers are necessary to neutralize these within their bodies. Crozier (1923) has cited evidence that indicates that active protoplasm is acid in reaction. Metabolism is related to size, and small animals metabolize more per gram than large. Animals have more or less automatic mechanisms for adjusting metabolism to changes in environment. The evaporation of perspiration in man is a means for cooling the body. Planarians are unable to increase their oxidative processes to maintain their usual metabolic rate when they are in a medium that is deficient in oxygen, but if changed to lower temperatures will gradually increase their rate of metabolism until it reaches that before the change. Recent investigations concerning the relations between the temperature of the bodies of various invertebrates and the media surrounding them showed temperatures of 0.05–2.44°C. above the medium. The earthworm reached a temperature within 0.05°C. of that of its surrounding medium within 2 minutes after a change. Animals show considerable individuality in their ability to adjust themselves to changes in environment. Child (1915) states that an individual is to be interpreted in terms of rate of reaction and of transmitted changes as manifested by the relations between protoplasm and the external world.

Circulating Body Liquids.—The circulating media within the bodies of animals have important relations to metabolism as carriers of nourishment, oxygen, and waste products. According to Dakin (1912), invertebrate marine animals have internal liquids that closely resemble sea water and that vary more or less as the surrounding medium varies, but freshwater and land invertebrates do not have blood that is like diluted sea water, and vertebrates, even in the ocean, have blood that differs from the surrounding water in salinity and (except in elasmobranchs which have considerable amounts of nitrogenous substances) in osmotic pressure. Blood pigments perhaps first circulated through the bodies of animals as waste products and later came to serve as carriers of gases for respiration. Active fishes have more hemoglobin and greater oxygen-carrying capacity than sluggish fishes (Hall 1929). Iron and copper are usually important constituents of the respiratory pigments in

blood. Among invertebrates hemoglobin is frequently characteristic of mud dwellers or animals living in poorly aerated water. It will hold thirty times as much oxygen as water. It is derived by many animals from chlorophyll, which contains four pyrrol groups, and that pigment is, therefore, often essential as a food in the environment.

Respiration.—Although oxygen is essential for all animals, there are many that are able to live indefinitely without free oxygen in their environment. Recent investigations show that several marine invertebrates, including the lobster, can endure prolonged sojourns in water containing little or no oxygen. Animals that live for long periods in the absence of free oxygen are not able to free all the oxygen from the compounds that they split up to maintain their metabolic processes. Planarians are not able to live in water that contains one-third its saturation capacity of oxygen. Many animals breathe through the outside of the body, but some have gills of various types for securing oxygen from the water, and those that breathe air commonly have lungs. Lepidoptera breathe through their broad wing surfaces (Portier 1933). A starfish breathes through its ambulacra and papulae and uses its skeleton as a buffer to neutralize acids (Meyer 1935). Various other means are employed by animals for securing oxygen: Certain fishes and amphibians swallow air and absorb oxygen through vascular areas in the alimentary tract; dragonfly nymphs and certain sea cucumbers breathe through the specialized walls of the cloacal chamber. The swim bladder of fishes was probably first respiratory and secondarily came to serve as a hydrostatic organ (Hora 1935). Some aquatic animals pass large quantities of water through their bodies, and this serves for respiration. The amount thus flowing through a finger sponge is 78 l. per day; Ascidia, 173 l.; Stichopus, 20 l. Some aquatic insects carry air below the surface; others utilize bubbles from aquatic plants and get oxygen in other ways. Animals that live in sandy beaches have many interesting adaptations for keeping dirt out of their respiratory chambers.

Tides and Respiration in the Atmosphere.—Flattely (1920) has suggested that the rise and fall of the tides played an important part in the development of life on land, some of the animals becoming gradually adjusted to air breathing by being periodi-

cally left out of the water. Along the seashore there is an interesting series of crustaceans, snails, and fishes—some living always below low-tide mark, some frequenting the 'tween-tide zone, and others living always above the water. These animals show gradations between gill breathing and lung breathing. Some crabs and snails can breathe through either gills or lungs. Shore crabs consume less oxygen in air than in water (Raffy 1935). A barnacle high up on a beach may be out of water nineteen-twentieths of the time and retains a little bubble of air inside the apex of its tightly closed shell.

Respiration in Air and Water.—Racovitza (1904) states that air breathers in water usually develop the following rhythm: (1) long inspiration, (2) long submergence, (3) return to surface, (4) long expiration, (5) rapid inspiration and expiration, etc. A duck shows outstanding resistance to the effects of submersion when compared with a hen. A duck with a ligated trachea is able to stay under water 23 minutes, but a hen dies after 3½ minutes. If only the head of a duck is submerged, the heart and the respiratory rate slow down, and the resistance is normal, but a duck with a ligated trachea that is kept wholly in air will live only 7 minutes (Huxley 1913). A hippopotamus can remain submerged 4 or 5 minutes; a manatee, 12 minutes. Diving whales are believed to descend to depths of more than a mile and may remain for more than an hour. They are subjected to great pressure but do not suffer from "caisson disease" (Howell 1930). Most air-breathing fishes can respire under water indefinitely if aeration is good (Hora 1935). Some aquatic insects are believed to absorb oxygen from the water and to visit the surface only to expel waste gases. Noble (1925) has shown that hairy frogs are adapted to cutaneous respiration and that lungless salamanders have no left auricle because they breathe largely through the skin.

Growth.—Growth may result from metabolic processes. It is increase in size—not development or increase in mass. It may be determinate and cease when the animal attains adult size, or indeterminate and only become slower in the adult. A blue crab molts fifteen times between the megalopa stage and the adult, increasing the diameter of the shell about one-third after each molt. Animals that do not shed their exoskeletons usually grow gradually, though all parts of the body may not increase

proportionally. The weight of a crab may double in an hour after molting on account of the rapid absorption of water. The blood before molting may constitute only 5 per cent of the body weight and 50 per cent after.

Rhythmical Rest and Activity.—Not only is metabolism limited by appropriate temperatures and other conditions, but it takes place in a more or less rhythmical way. Many insects and vertebrates, and even simple animals like corals, have regularly recurring periods of rest and activity which are commonly correlated with the alternation of day and night. The butterflies belonging to the family Lyncaenidae (Frohawk 1914) are said to rest with the head downward from about four o'clock in the afternoon until sunset, then sleep with the head up throughout the night. Certain animals kept continuously in comparative darkness appear to suffer no particular injury. For example, animals in mines may remain in good condition for years.

Regeneration.—Animals are in continual danger of disturbances in their physiological balance through injury by actual loss of parts or through chemicals that incapacitate certain functions. Regeneration helps many animals to adjust themselves to such difficulties. A Difflugia can reunite with parts of its body that have been separated from it but cannot fuse with fragments from other individuals. Many animals can grow parts that their bodies may lack. Autolysis also enables them to absorb injured parts that cannot be separated from the body. Child (1915) has shown that the ability to regenerate certain missing parts of the body, like the head of a planarian, depends upon the rate of metabolism in the body mass that remains after mutilation. Certain limiting factors, like low temperature, may so operate as to prevent regeneration of parts that require high metabolic rates.

Excreta in the Environment.—The excreta of animals often constitute an important factor in environment. Excretory products are usually toxic to the producer and by their presence may constitute a basis for succession. Trouessart (1901) says that animal hygiene has four chief aspects: (1) removal of feces and excretions, (2) removal of dead bodies, (3) aeration of habitats, and (4) preservation of provisions. Many animals cleanse themselves carefully before producing eggs or young. Honeybees leave the hive to defecate and produce air currents for

ventilation by waving their wings. Some types of bees have definite places in their homes for the deposition of feces, cadavers, and other undesirable substances; others cover objects with heavy coatings of wax. A pocket gopher has a latrine pit at one side of its burrow. Birds usually remove feces from their nests, probably both to keep them clean and to prevent the droppings from giving notice to predaceous animals of the location of nests (Thomson 1935). A lion does not eat the intestines of the

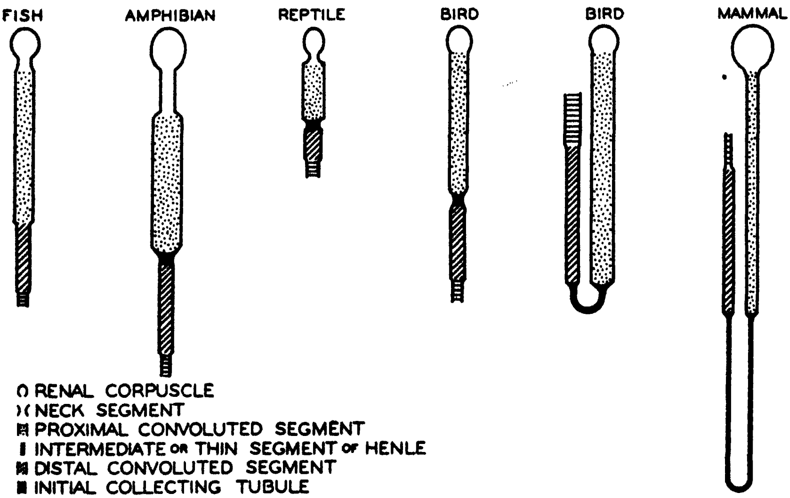


FIG. 20.—Diagrams of plans of kidneys of typical vertebrates. (*After Marshall, Burgess, & Harvey* 1933.)

animals that it kills, but cleanly removes and buries them. Some animals, such as termites and certain bees, are unusual in that they use their own excreta and those of other animals in the construction of dwellings.

Excretory Organs.—Various organs for eliminating wastes have been developed in animals, and these are adapted characteristically to environments. In the sea, animals that have body fluids that are isotonic with the surrounding water have no particular problem and often have no excretory organs (echinoderms). Marine animals in which body fluids are hypotonic to sea water secrete salt through specialized cells on their gills (teleosts) or raise the osmotic pressure of their body fluids by retaining urea (elasmobranchs) (Smith 1936). In freshwater a young salmon does not have salt-secreting cells on its gills; but, when it returns

from the ocean as a mature fish, they are well developed (Keys & Willmer 1932). In freshwater such animals as flatworms, annelids, crustaceans, and chordates often have elaborate kidney tubules which excrete water to keep the osmotic pressure of body fluids above that of the medium and also eliminate urea and other metabolic wastes. On land, excretory organs have been modified so as to permit reabsorption of water, and metabolic wastes are often excreted in concentrated or insoluble forms (Burgess, Harvey, & Marshall 1933, Marshall 1934). In vertebrate

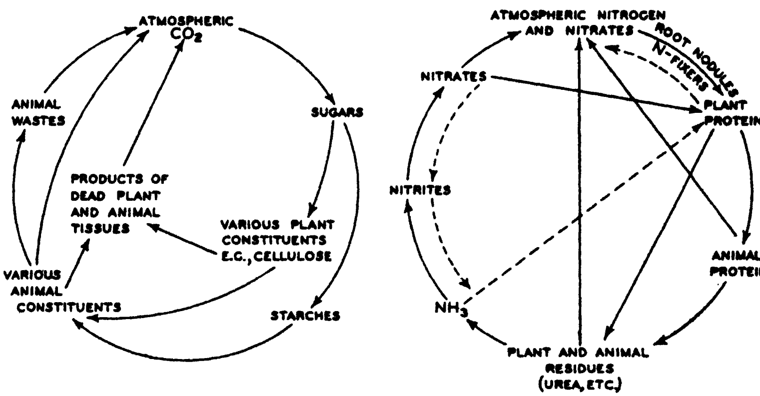


FIG. 21.—Carbon and nitrogen cycles. (*After Rogers* 1927.)

kidneys the glomerulus has been developed for water excretion (Fig. 20). It is degenerate in situations such as the ocean or deserts, where water is to be conserved rather than eliminated (Marshall & Smith 1930).

NUTRITION

Food.—A food is any substance that is taken into an organism and used for any purpose (Bayliss 1918). Foods furnish material for increase in size, for repair, and for energy. They must contain certain chemical elements that are essential for all protoplasm, and these must occur as particular compounds. Though a number of amino acids may furnish energy for metabolism, only a few types are of value as body builders. Plants are able to synthesize starches and sugars, but animals must have carbohydrates at least built up into glucose. The ultimate organic food resources of animals (Fig. 21) are always derived from

the plant kingdom. Chlorophyll usually is essential for the building up of simple organic compounds, and various bacteria are necessary for important steps in the degradation and synthesis of nitrogen compounds that may be used as foods. The production of nitrogen-containing compounds that may be used as foods for animals takes place largely on land and in freshwater; the shore waters of the ocean contain greater amounts of such compounds and of carbon dioxide than the pelagic and abyssal regions (Johnstone 1921). Light stimulates the oxidation of ammonium salts to nitrites in the sea (Zo Bell 1933, Rakestraw & Hollander 1936). In open waters such microscopic plants as diatoms and other algae elaborate organic substances. They are eaten by copepods and other small animals, and these in turn are devoured by larger animals. Thus "food chains" are maintained. Among other foods diatoms require carbon dioxide, silica, nitrates, and phosphates. These "fertilizers" sink into deep water as animals and plants die and disintegrate but are returned to the surface again at certain seasons by vertical currents. Aquatic animals often have food brought to them in the water that surrounds their bodies, but land animals usually are obliged to go to their foods. Except for vegetarians attached to plants and parasites there are few sessile animals on land, but there are many in water. On land the great body of green vegetation is easily able to take advantage of radiant energy. It generally manufactures foods of higher quality than plants in aquatic habitats, especially in the form of seeds, fruits, tubers, and other products that contain concentrated nutriment. Any organism requires general and special foods; there must be a balance of essential substances. Foods may be simple or complex, but they must satisfy the needs of the organism that assimilates them. They must include substances that can be oxidized to furnish calories for heat or work; compounds that may be built into body substances; vitamins and hormones that promote growth, reproduction, and other vital processes; particular salts; etc.

Food Values.—Vestal (1914) has summarized the characteristics that enable an animal to obtain food as: (1) structural, including such adaptations as the tongues of woodpeckers and the variation of the length of the alimentary canal in relation to different types of food; (2) physiological, relating to the range of

ability of particular animals to assimilate foods; (3) psychological, concerning the ability to select proper foods; (4) biographical, the timing of the life history to correspond with available food; and (5) numerical, the adjustment of the rate of reproduction to food supply. Mottram (1918) gives a list of the factors that control the desirability of food for a preying animal: (1) general hunger, desire for fuel; (2) special hunger, desire for variety—an animal may be satiated with one food but need another; (3) ease of access to food; (4) prevalence of food—one thing is usually hunted at a time; (5) palatability—an abundant food may be refused because it is distasteful. A dermestid beetle larva can subsist on hair, and this consists largely of keratin which is indigestible in the gastric and pancreatic juices of vertebrates. Small animals usually have higher rates of metabolism than large and reproduce more often. The "overturn" of food in them is relatively more rapid. A Daphnia can digest a protein and carbohydrate meal in half an hour. The amount of protease per gram of body weight in that little crustacean is two hundred times that in a pig (Hasler 1935, 1937). A food may be adequate in a sense and promote growth but be unsuitable as a basis for reproduction. For example, a mosquito (Culex) reared in a medium in which wheat flour was the nutrient supplied completed its life cycle in 50 days but produced small adults which averaged only 29 eggs per female, whereas females reared in a medium containing powdered spleen required 57 days to complete a life cycle but averaged 63 eggs each (Gaschen 1932). In this case differences may not have been due to nutritive values of foods alone. Such factors as reaction of medium and type of bacteria, other fungi, and Protozoa may have influenced growth and reproductive capacity.

Types of Food Habits.—It is difficult to classify animals according to foods eaten, because there are so many gradations, and so many animals fall in more than one class or change their food habits. Animals that have a narrow range of foods are called *stenophagous*, or *oligotrophic*, and those that eat a wide variety are *euryphagous*. Animals that are restricted to one food are *monophagous* in distinction from *polyphagous*, or *polytrophic*, species which eat many foods. Johnstone (1908) includes modes of nutrition for all organisms in five groups: *holozoic*, animals that prey on other plants and animals; *holophytic*, plants that live

on inorganic substances and carry on photosynthesis; *saprophytic*, organisms like yeasts and molds which ferment organic materials; *myxotrophic*, chlorophyll-bearing Protista and alga-containing animals which have two modes of nutrition in the same organism; *saprozoic*, organisms, such as a tapeworm, that absorb organic liquids. Folsom (1923) gives a most elaborate classification of insects according to food habits: *microphaga*, feeders on sugars and salts, with yeasts and bacteria; *sarcophaga*, flesh eaters; *coprophaga*, eaters of molds and bacteria; *mycetophaga*, consumers of fungi; *necrophaga*, eaters of dead animals; etc. Animals probably arose from plants when certain individuals instead of manufacturing their own organic foods began to eat their fellow organisms (Sandon 1932). Among Protozoa food appears to be of greater significance in determining relations to environment than other factors, for which there are generally wide ranges of toleration (Noland 1925, Sandon 1932). Flagellates are holophytic, saprophytic, and holozoic; among sarcodinians and ciliates there are no holophytic types, though some have symbiotic relations with algae. This indicates that flagellates are most primitive. Metazoans tend to become specialists in food habits, though even among such a group as insects there are many omnivorous types. Some early insects (cockroaches) perhaps fed on carcasses and vegetation, but some (dragonflies) were probably predaceous from the beginning. A museum pest (Trogoderma) will feed on insects, fur, feathers, cereals, nuts, castor beans, cayenne pepper; a cigarette beetle (Lasioderma) will eat almost any dried organic material, including pyrethrum, tobacco, leather, and talcum powder. On the whole, predaceous insects are not so specialized in feeding habits as parasites or vegetarians. Hunters such as solitary wasps and robberflies are frequently specialists; a particular species may capture only caterpillars, spiders, etc. Plant feeders are often very restricted in diet. Certain beetles, butterflies, and bees feed on only one family, or one species, of plants. Brues (1930) summarizes groups of insects according to food habits as:

Omnivorous, or Pantophagous
Herbivorous, or Phytophagous
Putrivorous, or Saprophagous
  Minimivorous, or Microphagous
  Fungivorous, or Mycetophagous

Carnivorous, or Zoophagous
 Predatory, or Harpactophagous
 Parasitic, or Biophagous

Birds and mammals show remarkable adaptations in beaks, teeth, and stomachs to particular types of food. Rodents have large incisors and no canines; carnivores have large canines and small incisors; snipes have slender beaks for probing bottoms; finches have stout beaks for cracking seeds.

Coker (1918) suggests that it is of fundamental importance from an economic point of view to rear together species that will not compete with each other for food. If this principle is followed, the productivity of an area may be greatly increased.

Types of Foods.—The importance of particular types of foods, of course, varies in different habitats. Proteins are the chief builders of protoplasm, but carbohydrates and fats are also essential. The presence or absence of water exerts an important influence in the distribution of many animals, and some of them often make long journeys to obtain salt. Though the necessity for vitamins has not been investigated throughout the animal kingdom, they are probably essential.

The distribution of animals often has direct relation to the availability of food, and particular foods are the leading factors in the lives of many animals. The oak is estimated to serve as food for 500 species of insects; apple, 400; clover, 200; corn, 200. In rivers the dead plankton that has settled down from the water above is a very important source of food for bottom animals. In Oneida Lake, Baker (1918) found that the plant- and detritus-feeding animals outnumbered the carnivorous species by a ratio of 337:1. Corals eat nothing but animal food, and their distribution is accordingly limited (Vaughan 1919, Yonge 1930, 1931, 1932). Megnin (1896) studied the succession of insects in cadavers. Sarcophagid flies began the feast, depositing eggs in natural openings. With butyric fermentation Dermestes and Aglossa were characteristic, but with ammoniacal fermentation the flies of the genera Pyophila, Ophira, Phora, Louchoea, Anthomyia, and the beetles Corynetes and Necrobia were present. When there were liquids in the cadaver the beetles Silpha, Hister, and Saprinus worked, and when it was dry tyroglyphid mites occurred. Very often animals that are closely

related systematically have quite different food habits. Leathers (1922) places chironomid larvae in six classes according to food habits: (1) feeders on bacteria, protozoans, small crustaceans, and diatoms that are strained by means of delicate nets from currents passing through dwelling tubes; (2) those straining food

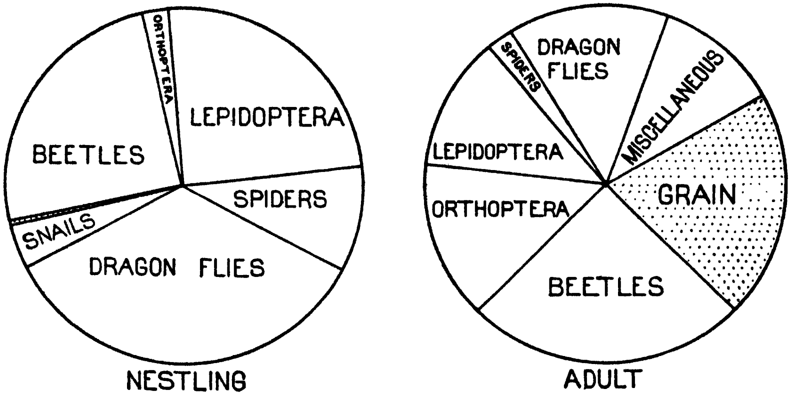


FIG. 22.—Diagram showing proportions of food of the red-winged blackbird *Agelaius phoeniceus*), young and adult. (*From Judd* 1900.)

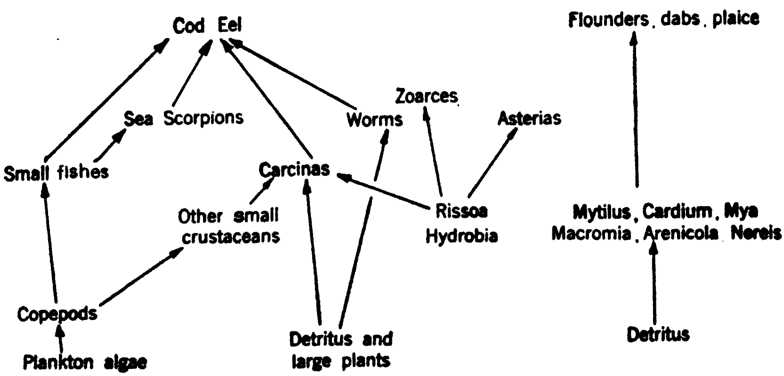


FIG. 23.—Blegvad's (1916) food chains for certain animals on the coast of Denmark.

from flowing water; (3) those living on accumulations of diatoms and plant debris; (4) feeders on floating aquatic leaves; (5) those eating filamentous algae; and (6) those moving about and actively seeking living food. Carabid beetles of various species consume four types of foods: (1) sucked animal fluids, (2) chewed animal and vegetable substances, (3) vegetable sucked and chewed mate-

rials, and (4) pollen and fungus spores (Forbes 1883). Bats of about the same size may be specialized feeders on insects, birds and mammals, fruits, or blood. It is well known that young animals of many species require entirely different foods from adults. Judd (1900) states that, except among doves and pigeons, all young birds are at first fed on an animal diet, which in general has a higher nutritive value than vegetable food.

Diets.—Students of nutrition have during the past few years greatly increased knowledge of food essentials, mostly by feeding experimental animals on rations of known foods. The last generation was interested chiefly in caloric values; this generation has turned its attention more to amino acids and vitamins. A gram of fat when burned to produce heat or do work produces 9.3 cal.; carbohydrate, 4.1 cal.; and protein, 4.1 cal. Protein molecules are composed of linked amino acids. The latter contain a basic amino group and an acid carboxyl group. They vary greatly in value as nutrients. Tryptophane and lysine, for example, contain groupings that cannot be formed in animals' bodies and are therefore valuable in food. Gelatin is an "incomplete" protein which alone will "not permit growth or even maintain nitrogen equilibrium in an adult animal" (Best & Taylor 1937). Glucose is of vast importance in carbohydrate metabolism; all organisms appear to be able to utilize it. Insulin is a hormone that permits cells to burn sugar. Fats, like proteins and carbohydrates, vary in nutritive value. They furnish energy and store it, insulate, and serve other useful functions. Vitamins are essential constituents of dietaries. At present six or more are recognized: A, antixerophthalmic; B, antineuritic; B_2 or G, antidermatitic; C, antiscorbutic; D, antirachitic; and E, antisterilitic. A, D, and E are fat-soluble; the others (B, B_2, and C) are water-soluble. A complete, balanced diet must contain foods that furnish an animal calories, carbohydrates, fats, proteins, salts, water, and vitamins. Animals have often been able to survive by invading habitats where they can take advantage of foods for which there is little or no competition, but such animals often become very specialized and are thus handicapped. Logs are eaten by certain insect larvae, which thus have to themselves a food that is indigestible and nonnutritious for most animals. A dermestid larva that lives on fur and dried skin avoids competition but must do much work to convert its food into

usable forms. It must even make water for its metabolic processes from inert substances such as keratin.

Dissolved and Particulate Foods.—There has been considerable controversy over the ability of aquatic animals to assimilate food from dissolved organic substances in the water around them. The older idea of Pütter (1907, 1923, 1924) that such foods are utilized by metazoans by absorption through external body membranes has not been supported by recent evidence. A protozoan (Chilomonas) is able to feed only on substances in solution and flourishes without light in media in which there are no organic substances. "It grows readily in sterile solutions containing $MgSO_4$, K_2HPO_4, $NaC_2H_3O_2$, and NH_4Cl" (Mast & Pace 1933). It will grow and divide faster if a salt containing compounds of sulphur is also present (Mast & Pace 1934, 1936). Paramecium will grow in bacteria-free media containing salts and organic materials (Loefler 1936). The fact has been stressed that certain small plankton animals, such as Daphnia (Hasler 1935) and Artemia (Bond 1933), are structurally and physiologically equipped to acquire, digest, and assimilate particulate rather than dissolved food substances. Some microscopic animals undoubtedly are able to feed on bacteria and other nannoplankters. There may be great bacterial activity in sea water that has been freed of all particulate matter (Keys, Christiansen & Krogh 1935). Bacteria are capable of decomposing even such resistant substances as chitin, aerobically or anaerobically, and thus release organic compounds (Steiner 1931). Copepods can live in paper-filtered water that contains only bacteria and other minute organisms. Some mosquito larvae will not develop in water that does not contain bacteria or other fungi (Hinman 1933). Such highly organized animals as frog tadpoles (*Rana pretiosa*) develop normally when in water with no particulate food except bacteria (Burke 1933). In a wood-boring beetle Payne (1931) showed a remarkable case of dependence on fungal food. She found that without fungi the larvae of certain wood-boring beetles did not pupate but still remained alive, so that they lived for several years, as much as ten times their usual length of life. If the larvae were given food fungi, they soon pupated and in a short time became mature. Such facts indicate that many animals are more or less dependent on fungi which may develop in various media, rather than on dissolved organic sub-

stances. Furthermore, as Krogh (1931) has well pointed out, many organic substances in solution are waste products and not readily assimilable; plankton algae do not discharge carbohydrates into water; and food necessary for aquatic animals is generally present as organisms or organic detritus. Protozoa and perhaps sponges may utilize dissolved foods, but the integuments and gills of metazoans are usually impermeable to organic substances. Krogh stresses the fact that dissolved organic substances utilized by tadpoles, mussels, and starfishes are absorbed through enteric membranes, not through the exterior. Daphnia has been grown to maturity in water that contained no particulate matter but did have colloids (Gellis & Clarke 1935). Hinman (1932) reared mosquitoes from egg to maturity in sterile water without particulate matter, but he was unable to do this when colloids were not present. He found that a larva passed water equal to twenty to two hundred times its own volume through its alimentary canal daily. From this it absorbed enough nourishment through its enteric membranes to promote growth.

Amount of Food Required.—The amount of food necessary to maintain an animal varies considerably, even among individuals of the same species. The size of many animals depends more or less on the amount that they have been able to obtain and assimilate. If two starfishes hatch at the same time, one may be a hundred times as large as the other after 3 months. The largest jellyfishes are found in cold seas, where there is the most abundant supply of food. An oyster strains about 250 l. of water per day to obtain its food. A Didinium may swallow a Paramecium that is ten times its own bulk. A caterpillar may eat twice its own weight daily, and a flesh-eating larva has been reported to eat two hundred times its own weight in 24 hours. A hummingbird has eaten twice its weight in sugar in a day; a goosefish may eat half, and a mole two-thirds, of its weight in the same time. Kluijver (1933) made careful observations on the food of nestling starlings. One group was fed 6,895 times by its parents; another, 7,668 times. These young birds ate 17,933 objects of 313 species, 267 of which were insects. During its first day after hatching, a young starling ate 144 mg., about half its own weight; during the tenth day, 853 mg. A family of marsh hawks observed by Breckenridge (1935) ate

about 63 lb. of food during life in their parents' nest. The black swallower is able to ingest other fishes that are larger than itself (Fig. 24). It has been estimated that the larva of a moth before it pupated ate 86,000 times its own weight at the time of hatching. The renewal coefficient for the food in the alimentary canals of certain cladocerans has been found to be from 15 to 60 minutes. The rate of digestion in different animals varies greatly: a Didinium will digest a Parmecium in

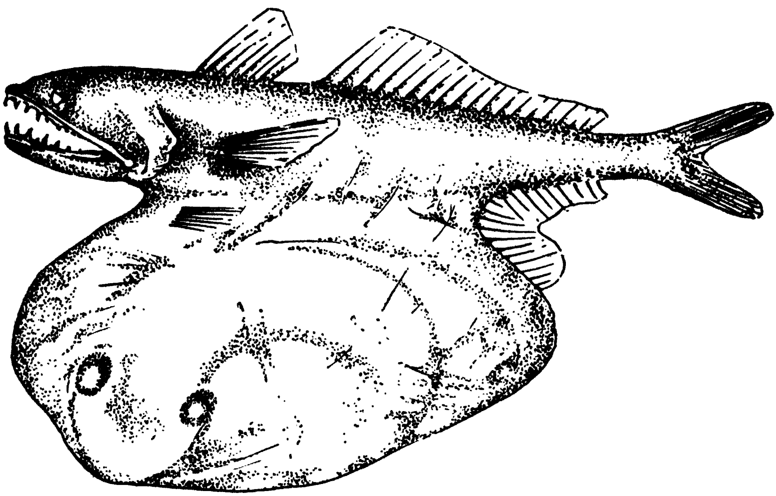


FIG. 24.—The black swallower, *Chiasmodus niger* Johns., a deep-sea fish which devours other fishes often larger than itself. (*After Murray & Hjort* 1912.)

2 hours and eat another; a cockroach may take 2 months to absorb a large meal of fat through the wall of its intestine. Araneid spiders have been found to eat about 2.5 fruit flies per day (Nebel 1918). The Danish naturalists estimate that a bottom fish eats about one-thirtieth of its own weight daily during 300 days of the year, thus consuming a total of about ten times its own weight of flesh. They believe that it takes about 18 kg. of food to produce 1 kg. of plaice, as against 3.4 kg. of food for 1 kg. of trout as estimated by British investigators. Freshwater fishes at 20°C. consume an amount of food equal to about 6 per cent of their body weight and volume per day (Pearse 1924). Of course the rate of digestion of a fish, or any other poikilotherm, increases at higher temperatures, approximately according to

Arrhenius' Law (Nichols 1931). A fish consumes three times as much food at 20 as at 10°C. (Hathaway 1927). The optimum temperature for the action of its digestive enzymes is about 37°C. (Kenyon 1925). In Bermuda the amount of bottom material that passes through an adult Stichopus is 6 to 7 kg. dry weight, per year.

Starvation.—Some animals require a continual supply of food for their maintenance; others can fast for days, months, or years. The length of time that certain animals have been kept without food is as follows: lobster, 7 months; dragonfly nymphs, 3–8 months; puffin, 28 days; albatross, 35 days; bowfin, 20 months; sea elephant, 1 month; dog, 117 days. Certain beetle larvae, ticks, and leeches can live more than 4 years without food. The form and the structure of some animals are dependent to a considerable degree on the amount of food received, and many fasting animals not only decrease in size but change their form when without food. An amoeba may live more than 20 days without food and decreases in size 95 per cent (Mast & Hahnert 1935). Planarians have been known to decrease in size to half their original length and one-hundredth of their original volume while fasting. Other invertebrates also undergo remarkable reductions in size under similar conditions, and many are even able to regenerate lost parts of their bodies. The museum pest, *Trogoderma tarsale*, has been kept alive without food for over 4 years, continuing to molt at intervals but decreasing in size after each molt. Cladocerans reared in highly diluted nutritive media grow more slowly, live longer, and produce fewer young (Ingle 1934, 1935). There are some animals that regularly fast for long periods: a bull seal goes without food for 3 months while guarding his rookery. Certain male ticks and rotifers never eat but go through their entire life cycles on the nourishment that they receive from an egg.

Selecting and Procuring Food.—Animals in general select particular foods from their environments. Many food specialists have elaborate adaptations for securing and handling foods. Yet animals that are evidently fitted for some special type often depart from what may be expected. A dog often eats grass; a vegetarian sea urchin may capture and devour a fish (Parker 1932). Foods eaten by animals may vary at different seasons or in different years (Errington 1935, 1937). Nestling marsh hawks

are fed entirely by their mother, but 80 per cent of the food that they eat is captured by their father, who transfers his offerings to his mate on the wing (Breckenridge 1935). A feeble oyster can capture and digest such thick-skinned and active animals as nematodes and crustaceans (Nelson 1925). Many marine plankton feeders trap small animals in mucous threads (McGinitie 1937). Clams in general have elaborate ciliary-muscular sorting mechanisms for procuring food (Graham 1930, 1931, Yonge 1931). Certain birds periodically shed and cast out the linings of their gizzards, the character of which changes with seasonal variations in available foods. Insects often show remarkable specializations for particular foods. They may be suckers or gnawers. Some species are strictly diurnal or nocturnal, and their activities may even be restricted to certain hours. Some of them readily adjust themselves, so that their selection of appropriate foods depends upon special colors, odors, or previous experiences with favorable or unfavorable substances (Sladden 1934, McIndoo 1935). The geographic distribution of many animals is limited by the location of foods. The vulturine fish eagle in Africa is found where there are oil palms (Moreau 1933). Certain butterflies are definitely associated with particular food plants, and the phylogeny of the insects and plants shows parallel evolution (Kuznezow 1930). There are endless adaptations for finding and securing foods. Torrential caddis-flies spread gauzy nets from which they scrape off organisms brought by currents. Archerfishes with drops of water shoot down flies from vegetation to surface film where they may be secured. Anglerfishes display luscious lures to attract their prey.

Stores.—A considerable number of animals store food. This is often apparent in localities where there are clearly defined cold and warm, or wet and dry, seasons. Stores of food are gathered by some animals in order to provide food for their offspring. Squirrels bury nuts in the ground or carry them into natural cavities where they may be available for use in winter. The California woodpecker drills holes in tree trunks and hammers acorns into the cavities. In winter it eats the acorns and certain grubs that infest them (Ritter 1921). Solitary wasps sting and paralyze spiders, caterpillars, and other insects. These they store in burrows or specially constructed cells with their eggs. Larvae are thus provided with food when they hatch. Social

hymenopterans gather seeds, pollen, honey, and other products. These they store away to be used as food for themselves and their larvae during periods of scarcity.

Food and Reproduction.—The reproductive activities and life cycles of many animals are markedly influenced by the character or amount of food available. Budding and other types of asexual

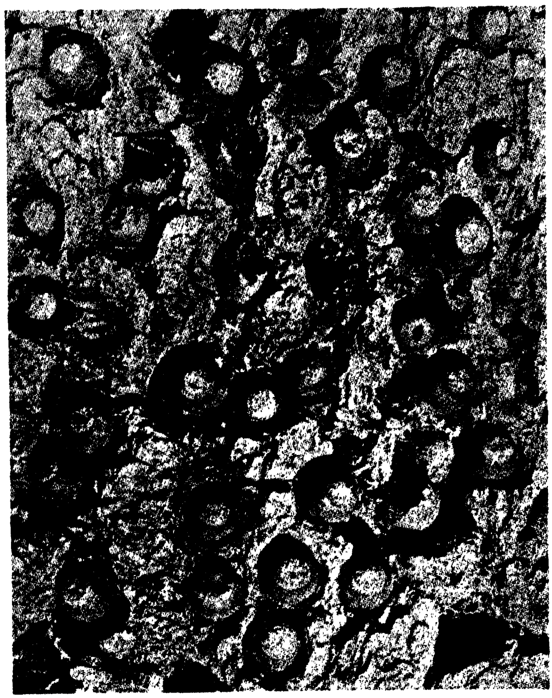


FIG. 25.—Acorns stored in a tree trunk by a California woodpecker, *Melenerpes formicivorus bairdi.* (*From Ritter* 1921.)

reproduction are generally inhibited by inanition, and sexual reproduction is stimulated (Jackson 1923). Among aphids there is good evidence that parthenogenetic females are succeeded by those that produce fertilizable eggs and male-producing eggs when the food supply fails. Rotifers have been similarly influenced by variations in the supply of manure or of certain algae. A caterpillar that is underfed lives an unusually long larval life and spends a relatively shorter time as a pupa. Jackson (1923) asserts that the gonads of animals are generally resistant to inanition. Starvation, however, is known to inhibit the development of the

gonads in Drosophila. It is also an important influence in the development of castes among certain social insects.

Food as an Environmental Factor.—As a factor of the environment, food has various relations to animals. For most animals it is a necessity which serves as a continual spur to activity. The finding of food and its capture constitute the daily, year-round business of most animals. But there are also periods when food may take a secondary place and other factors become more important. During the breeding season a fish on its spawning ground usually contains no food. Its reproductive activities dominate. A salmon may swim hundreds of miles up a river without eating. Food chains are characteristic of every habitat. Plants are at the base of these. Some very large animals, such as elephants and buffaloes, feed directly on them, and the chain is thus short and simple. Other chains begin with microscopic plants, which are eaten by small animals, and these initiate a series in which predators grow progressively larger and fewer, *e.g.*, from diatoms, copepods, molluscs, fishes, to seals. At the beginning of such chains animals are small and multiply rapidly, whereas at the end animals are large and live long. On the other hand, parasites in food chains tend to reverse such size and number relations because they are usually smaller and more numerous than their hosts; *e.g.*, lice are more numerous and smaller than dogs; mites are small and many compared to lice; Protozoa are minute and may invade even a small arthropod in numbers; bacteria may live in Protozoa. A group of animals may unite in attacking an animal that is larger than any one of them. A band of wolves can bring down and devour a deer.

Food Resources.—Large areas of the earth which present extensive, rather uniform environments are able to supply considerable quantities of food. Great fisheries are in oceans, lakes, and rivers, not in brooks and pools. Wide prairies and savannas may support herds of buffalo or cattle. Great forests harbor numerous deer and moose. All these great resources depend on light, photosynthesis, and food chains adjusted to an extensive and harmoniously balanced environment.

REPRODUCTION

Functions of Reproduction.—Reproduction in animals serves two functions: (1) to increase the number of individuals and

(2) to produce individuals that have combinations of characteristics that differ from those of their parents and that may enable them better to survive in the particular environment in which they are produced. Multiplication by fission, budding, and other similar methods may depend to some extent on environment but usually has no very complicated relations to it. Child (1915) has shown that asexual reproduction is due in many cases to the physiological isolation of parts by the growth of an animal's body to such an extent that portions of it are beyond the influence of the controlling region and thus may readily become independent. Conjugational reproduction, however, has many complications that are concerned with various phases of the fusion of gametes, cross-fertilization, dimorphism, courtship, care of young, and other activities.

Breeding Instincts.—During the breeding season many animals have instincts that make reproductive activities dominant. If feeding is antagonistic to breeding, the former is often neglected. Many species also become an easy prey to enemies during the excitement of the breeding period. Among some dioecious animals individuals of the two sexes may never see each other. The males of certain salamanders, myriapods, and pseudoscorpions deposit spermatophores which are later picked up by females. Among species that mate, many expedients are employed to bring two individuals of opposite sex together. The male fiddler crab waves his bright claw before the female; spiders dance and posture; birds sing and display recognition marks; a male Cecropia moth finds his mate by her odor, though she be a mile away. In some species eggs are fertilized after they leave the body of the parent; in others impregnation is internal, and more than a year may elapse before young are born. Among some species of fishes and birds the males early invade the breeding grounds and await the coming of females.

Seasons for Reproduction.—Reproductive activities are commonly cyclic in their nature and often show correlation with annual, lunar, or other rhythmical environmental changes. Many birds migrate north, court, select a nesting site and build a nest, lay eggs, incubate, rear young, migrate south, feed, and rest—then repeat the cycle. In such a cycle of activities the sexes may play slightly different roles. For example, the male often arrives on the breeding ground first and selects a general

area; the female follows, selects the actual site for the nest, and does most of the building. The reproductive cycles of birds are usually closely correlated with seasonal progression, but those of many other animals are not. Recently considerable evidence has been accumulated which shows that length of day has marked influence on the endocrine glands and breeding of birds and mammals. The fish Gambusia brings forth its young without apparent relation to temperatures, and hydroids often pass through several reproductive cycles while environmental conditions remain reasonably uniform. On the other hand, oysters spawn at about the same temperature throughout their range (Orton 1920, 1931, Nelson 1928, Prytherch 1929), when temperatures reach 20°C. Some events in a reproductive cycle, though they may be correlated with definite seasonal periods, take place but once. When a female pocket gopher is mature, the bones on the ventral side of her pelvis are resorbed, so that she may bear young; a salmon spends a few years in the ocean, then migrates up some river to spawn and die (Belding 1934).

Stimuli for Reproduction.—Changes in environment often release potential reproductive functions. It is well known that the presence of small quantities of certain substances help in the fertilization of the eggs of many animals. On the other hand, extracts from the larvae of the sea urchin, *Arbacia punctulata*, will inhibit the development of eggs of the same species. Ciliates apparently produce a substance from their own cells that accelerates fission rate, but a small volume of culture medium and accumulation of excretion products will retard it (Greenleaf 1926). If a squid spermatophore comes in contact with the sea water, it discharges its spermatozoa; a Crossobothrium proglottid, passing out of a sand shark and encountering the same stimulus, undergoes active contractions and sheds its eggs. Polypterus goes out into the surrounding lowlands to spawn when the Nile overflows. Certain marine annelids spawn when the proper season and sign of the moon arrive. Some animals mature their reproductive products and, when there is a failure of food or when other unfavorable circumstances develop, resorb them again without producing offspring.

Productivity of Animals.—The rate of development and increase through reproductive activities, of course, varies greatly. Krogh (1914) has shown that the rate of development of amphib-

ians, fishes, insects, and echinoderms varies in relation to temperature according to van't Hoff's Law. Changes in moisture, temperature, and oxygen supply are important in causing variations in developmental rate. Peterson (1918) during his studies off the coast of Denmark showed that there was not a great renewal of the stock of marine animals each year but a large production in certain favorable years, which recurred at more or less regular intervals. The annual production of some animals is enormous. A blue crab has been estimated to carry 1,750,000 eggs at one time; an adult cod averages about 4,398,700 eggs per year; a female termite in her prime may lay 60 eggs per minute. Oysters have been observed to produce 55 to 114 millions of eggs each (Galtsoff 1930). On four spawning grounds in the Strait of Georgia the Pacific herring annually produces 8 to 75 billion eggs, 1 to 9 million fishes participating. Only about 0.1 per cent of these come to maturity, though 95.0 per cent hatch (Hart & Tester 1934). In general, the number of young produced is inversely proportional to the amount of care given to the eggs and young, but there are many exceptions. The size of birds' eggs is roughly related to the length of time that they remain in the nest, those that remain for longer periods generally being larger. Some animals increase the number of their offspring by polyembryony. This may result merely in a pair of twins or in more than a thousand individuals from one zygote (Patterson 1927).

Length of Breeding Periods.—Breeding may extend through long periods if conditions are favorable. Certain species of freshwater amphipods produce young for 152 to 299 days out of each year. In deserts, on the contrary, where conditions for reproduction are rather unfavorable, animals tend to live longer and to produce a few offspring which are carefully reared. Orton (1920) found in the North Atlantic that breeding periods, in general, began at the close of periods of maximum and of minimum temperatures. Frogs gather in particular breeding pools which they select with care, often leaving a pool in which they have hibernated and traveling some distance to another. They may congregate in breeding pools for several weeks before spawning (Savage 1935). Up to moderate altitudes, especially in districts subject to orographical rainfall, spawning is earlier the higher a pond is above sea level.

Breeding and Food.—Among birds there is a striking relation between the availability of food for the young and the size of the nesting area. Birds like plovers, which have difficulty in securing sufficient insect food for their young, defend large nesting areas; whereas certain sea birds that have no difficulty in securing an abundance of fish from the neighboring ocean crowd so close together that they have barely room to sit on their eggs.

Care of Offspring.—Most animals are not only able to produce offspring but also have some means for insuring their survival. There is, however, every degree of variation in this respect. A cod produces millions of eggs and leaves them unprotected on the surface of the ocean, enough nourishment being present within each egg to provide food for the young fish until it is able to shift for itself. Some animals cease their reproductive cares when they have deposited their eggs in proximity to a food supply for the young. Pratt (1912) reared insects from cow manure and obtained 31 species of Diptera, 17 of Coleoptera, and 1 of Lepidoptera. The tumble beetle rolls a ball of manure to a secluded spot and buries it with its eggs, thus giving its larva both protection and food. Girdling and leaf-rolling insects make similar provision for their larvae. The female leaf-cutter ant while establishing a new colony feeds herself and young on her own eggs and also raises fungus on manure beds for food. Bees, wasps, and ants generally build nests which they store with food and in many cases feed their young. Many animals though not always attending to the food supply of their offspring furnish special means for protecting them. Some frogs build nests attached to leaves over water, and the tadpoles drop into the proper habitat when they hatch; others lay eggs in masses of froth, far from water. Spiders and myriapods inclose their eggs in carefully constructed cocoons. McCook (1889–1893) says that there is a definite relation between the protective value of spider cocoons and the amount of care given them by parents, the poorly constructed cocoons being watched or carried by the parents. Aparity occurs in certain mites, *i.e.*, the young hatch within the body of their mother and feed on her tissues until they make their way out (Jacot 1933). Birds brood their eggs and young, thus providing protection from cold, heat, and rain; the young are also fed and excreta are removed from the vicinity of the nest. Penguins cooperate in caring for the eggs of parents

who go to the sea to feed (Bennett 1927). They have such strong brooding instincts that they are continually trying to steal eggs.

There are many animals that guard their offspring or actually carry them about with them. The mound-building birds of Australia, though escaping the tiresome routine of keeping their eggs warm with their own bodies, attend their incubators with watchful care, opening up the mound to admit radiant energy from the sun and adding or removing rubbish as humidity varies. A skink remains with her clutch of eggs in a rotting



FIG. 26.—A skink, *Eumeces fasciatus* (L.), in a rotting log with its eggs. (*From Ruthven* 1918.)

log and, if one of her treasures is moved a little distance, she moves it back with the rest (Noble & Mason 1933). The male hellbender guards his nest, eating eggs from it but exercising a generally protective function by his presence. Pycnogonids, seahorses, crayfishes, certain frogs, and other animals carry their eggs and often also their young about with them. A cockroach in India carries its young about under its wings (Pruthi 1933). Many freshwater fishes clear spaces or construct nests which they guard and keep clean (Breder 1936). The male gaff-topsail catfish carries his eggs in his mouth for nearly three months and probably takes no food during that time (Gudger 1918).

A great advantage accrues to those animals that pass a period of adolescence during which they are fed and gain experience

under the tutelage of their parents. The male freshwater dogfish not only builds and guards a nest but swims about with his young for a time after they hatch. Mammals give their young a prolonged period of nourishment and protection within their bodies and attend them afterward until they attain some degree of maturity (Tomilin 1935). The young of birds fall into two

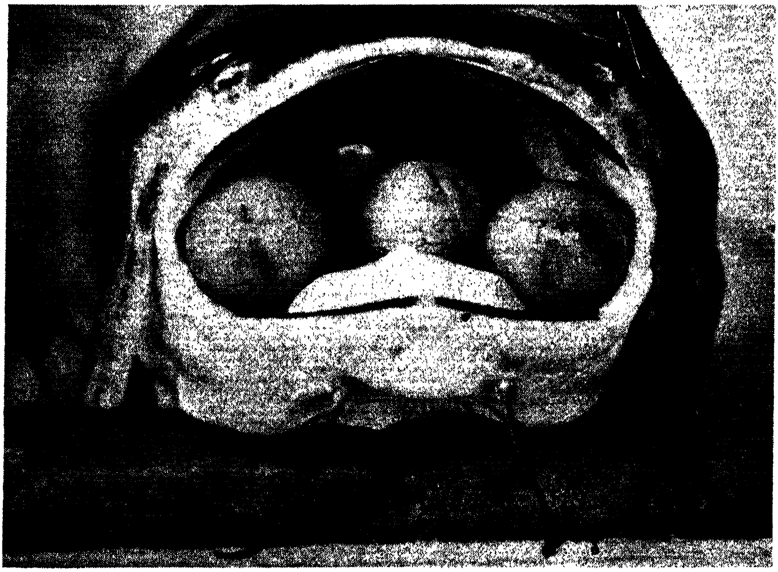


FIG. 27.—Male gaff-topsail catfish carrying eggs in its mouth. (*From Gudger 1918, courtesy of the American Museum of Natural History.*)

classes: precocious, which are able to shift more or less for themselves soon after they hatch; and altricial, which pass a period of helpless development during which they are cared for by their parents.

Length of Life.—The length of life of animals varies within wide limits. Some Protozoa exist as separate individuals for only a few hours; an elephant may live for 200 years. There is no general correlation between size, activity, complexity of structure or "constitution," and longevity. However, small species of animals usually live shorter lives than do larger forms. Life has been said to be interaction between nucleus and cytoplasm. When cytoplasm becomes too much reduced, a cell often grows old and dies; an increase in the relative amount of cyto-

plasm may rejuvenate a cell. "Anything that decreases the interchange between nucleus and protoplasm leads to senility; anything that increases this interchange renews youth" (Conklin 1913). Poikilotherms usually live longer at low than at high temperatures (Janisch 1929, Whitcomb 1932). Some animals that normally live short lives may have their usual span prolonged by adverse conditions. Tiger beetles are usually annuals, but in Canada, where the larvae do not have time to acquire sufficient food to complete their growth in one season, these insects are often biennials. In general, animals that live for long periods produce fewer offspring and bear them at less frequent intervals than those that live for a briefer time. In many species of animals males live shorter lives than females, and some live only long enough to exercise their fertilizing functions. Female insects are likely to live longer than usual if they do not lay eggs. Moths that mate early have been shown to live shorter lives than unmated individuals. Some animals die soon after reproducing. In many species large and small individuals are more apt to remain unmated than those of average size, though there are some instances, as in the case of the male walrus, where extremes of size are of advantage in securing mates. Where a species has reached a state of equilibrium in a particular locality the death rate about keeps pace with the production of new life. Cary (1918) found that reef gorgonians seldom died of old age; the corals required 2–5 years to reach medium size, and about one-fifth of the population died from various causes each year.

Influence of Environment on Type of Reproduction.—The type of reproduction or the duration of a particular type may be controlled to a considerable extent by environment. There has lately been some controversy concerning the "necessity" for conjugation among protozoans and the ability of various protozoans to live in culture media of unvarying composition. It has been shown that some species thrive for great numbers of "fission generations" in unvarying media and that others apparently become weak and die out if the environment does not vary. Some species have been kept active for several thousands of generations without conjugation when the culture medium was varied and in some instances when it was not (Woodruff 1932, 1935, Spencer 1924). Among rotifers, crustaceans, and insects are many species in which a series of parthenogenetic generations

alternates with amphigenetic generations, and it has been possible in some cases to determine certain of the causes that induce one or the other type of reproduction. By varying food and temperature in such cultures, investigators have been able to maintain them without the appearance of sexual individuals or to cause such to appear at rather frequent intervals. By parthenogenetic reproduction alone rotifers have been propagated for over 500 generations, and aphids for over 4 years. Other factors than temperature and food may be important in initiating new types of reproduction. For example, Mrázek (1913) described an oligochaete that propagated inside a cyst which was formed when the water in which it lived dried up. Notwithstanding the nice agreement that the reproductive phases of many species show with varying conditions of environment, there are some species, even in groups where such agreements are common, in which the types of reproduction take place without particular relation to changes in environment. Green (1919) found that, although *Simocephalus vetulus* was apparently "indefinitely viable parthenogenetically," when amphigenetic individuals appeared they did so in no definite order, even from the same mother, and in cultures parthenogenesis could never be wholly inhibited by varying conditions.

Inbreeding.—There has long been a superstition that the inbreeding of close relatives is invariably injurious to a race, but recent experiments have shown that some animals can be inbred for many generations without apparent loss of virility, and in some experiments the stock appeared actually to improve. It has also been shown that cross-fertilization is not essential in some hermaphroditic animals. *Limnaea columella* has been reared by self-fertilization for 20 years without apparent loss of vigor in the stock (Colton and Pennypacker 1934). Conjugation and cross-fertilization in many metazoans apparently serve somewhat the same purpose as encystment, hibernation, and similar phenomena. In times of stress, mixings from different stocks produce more types of variants, some of which may be able to pass over an unfavorable period. In other words, changes in environment, at least in a number of instances, appear to induce changes in the modes of reproduction of animals and probably also initiate the temporary dominance of new types of variants because these better fit the changed environment.

Life Histories.—There are stages in life histories that appear to develop at a certain rate, more or less without relation to the condition of the environment. Artemia eggs do not hatch sooner if kept at higher temperatures. The palolo worm gives off more carbon dioxide as the spawning season approaches. Treadwell (1915) holds that this indicates an increase in metabolism and believes that egg laying is due to internal, as well as external, stimuli. A serricorn beetle of the genus Micromalthus passes through a very complicated life history—including three types of larvae and two or three generations—in a rather uniform environment in rotting wood (Barber 1913). On the other hand, there are many stages in life histories that are more or less dependent on conditions in the environment. Swingle (1922) maintains that iodine and tyrosine are essential as constituents of the food of frog tadpoles if metamorphosis is to be completed. The length of the pupal life of insects is often dependent on the rate of evaporation of water, and some pupae are surrounded by a layer of gum which retards evaporation (Folsom 1923). Baker (1918) found a relation between age and the depth at which certain species of molluscs were found in Oneida Lake. In termites and ants the attainment of certain stages in the life cycle appears to depend on the living environment. When royal termites are present in a nest, substitute forms do not lay eggs; but if the royal forms are removed, the substitutes mature. Winged forms do not appear in nests of the carpenter ant until colonies are two years old and until about 2,000 workers are present (Pricer 1908).

Some events in life cycles come as the result of the attainment of a particular degree of development. Different species of salmon spend from two to five years in the ocean. They then migrate into streams, apparently in the full vigor of maturity, but after breeding become senile very rapidly and soon die of old age (Moore 1919). An eel hatches 500 fathoms deep in the ocean, lives a pelagic life for a time, then invades freshwater for a period of years, and finally returns to the ocean to breed. Herrick (1909) describes three interesting stages in the development of the young cuckoo after hatching: (1) a period of more or less helpless infancy up to the sixth day, (2) the complete quill stage, and (3) the climbing stage, characterized by the desertion of the nest and the development of feathers, between the

seventh and seventeenth days. The young do not show fear until the end of stage 2, and the last one to leave the nest may be deserted because the instincts of the parents are diverted by attention to those already in the bush. The development of a cuckoo is associated with the progressive development of cyclical instincts in both young and parents.

Reproduction and Environment.—An animal starting in life inherits a capacity to develop in a particular way. In some cases development depends on the encountering of a series of very complicated environmental conditions in a definite order; in others it takes place in a very uniform environment where surrounding conditions change little or not at all and the progressive changes that take place originate from stimuli within the animal itself.

PROTECTION

Survival.—Animals are continually beset with dangers: Environment may change beyond their limits of toleration; there may be a less pronounced change which does not actually make it impossible to exist but makes it more difficult because conditions become more favorable for a competing animal; predatory species continually devour a certain percentage of the population; and insidious parasites wait for opportunities to invade the bodies of their hosts. Marked changes in environment may completely upset the established balance in a habitat; some species may decrease or die out completely, and others increase. The animals in any habitat usually have means for adjusting themselves to usual changes. When the water in a pond dries up, certain planarians roll up, especially so as to protect the anterior end, and, surrounded by mud and secretions from their own bodies, are thus able to survive for a time.

Predaceous Animals.—The world of preying animals has various means of capturing its food. An archerfish shoots drops of water; a crocodile lurks immobile and drags its prey under water; a python hangs waiting in a tree; a vulture circles 2,000 ft. above the earth and with its keen eyes patiently watches for something to die; an angler displays baits to attract little fishes; a spider spins elaborate snares. Predatory animals continually watch for an animal that is at a disadvantage. Wolves follow a sick or injured buffalo and wait for it to die;

dragonflies are easy victims when they are emerging from their nymphal skins. Ants frequently eat their injured fellows (Hingston 1920). It is well known that elephants, cattle, and other animals often turn on weak or wounded individuals in their herds.

Escape from Enemies.—Animals employ a great variety of means to escape from predators: agility or speed in flight; habits of resting in open places, so that approaching enemies may be readily seen; hard shells on the outside of the body (insects, turtles, molluscs, hermit crabs, armadillo, etc.); electricity (torpedo, electric eel, etc.); distasteful or irritating odors or flavors (skunk, millipeds, various insects, etc.); autotomy (lizards, crustaceans, brittle starfishes, etc.); death feigning (walking stick, many bugs, opossum, etc.); spiny or slippery exterior (spiny lobster, sea urchins, eels, etc.); alarming or startling appearance (puss-moth larva, etc.); concealing or warning coloration and mimicry; active resistance (clawing, scratching, biting, etc.); the association of two species together, one or both having some protective qualities (hermit crab with anemone, etc.); the defense of colonies by special protective individuals (soldiers among ants and termites, stinging individuals in hydroid colonies, etc.); the use of protective devices taken from other animals (nematocysts of coelenterates used "second hand" by molluscs and flatworms, etc.); resorting to isolated or inaccessible places, such as burrows, houses, islands, or cliffs; luminosity (possibly of protective value to some pelagic, marine animals); behavior by parents that simulates injury and attracts predators away from eggs, young, or mates. If such measures as the last are not effective, some species of birds stage a mock combat among themselves to attract attention.

Means of Defense.—The dependence of animals on some of these means is remarkable. A walking stick or a giant water bug while in a death feint will not move, even if its body is cut in two. The latter assumes two death-feigning attitudes, both unlike the position assumed in actual death. By appropriate stimulation it has been made to feint 38 successive times for a total of about 8 hours. A scallop's chief danger is the starfish, and it swims precipitately away if a dilute extract from its enemy is squirted into the water about it. Certain beetles of the genus Stenus escape from floods by "skimming" on the surface of the

water. This they are able to do by secreting a substance at the posterior end which, on account of differences in surface tension, forces them rapidly forward. Such animals as horses, deer, and houseflies depend largely on the acuteness of their senses and their speed for escaping from enemies. Birds hastening south in their migrations may attain a speed of over 100 miles per hour. Sometimes slow stupidity has better survival value than agile astuteness. Animals do not fall into two classes, protected and nonprotected, but protective devices are rather to be classified as more or less efficient. Animals are not protected from all dangers but are usually suited particularly to escape those of certain types. It is believed that the elephant is limited in numbers chiefly by the harassing of little insects, and of course cattle and men are absolutely unable to live in certain parts of Africa on account of the parasites carried by tsetse flies.

Homes.—The dwelling places of animals serve as refuges for developing young, as prisons to prevent adolescents from wandering, as places for the training of the young, for the storage of food, etc. Homes are often concealed or placed in inaccessible places but may be conspicuous, particularly in gregarious or social species. The home and its situation are more or less distinctive for each species. In some cases homes are merely spots which appear much like other similar places. Birds choose a secure roosting site with considerable care and often return to the same spot night after night, apparently to avoid the trouble of finding a new place. A nighthawk builds no nest but lays her eggs on the surface of the ground, and yet she recognizes this place as home. Some coliad larvae rest on the under surface of leaves near the center. They go to the edge of a leaf to feed but spin a thread in order that they may return directly to their resting spot. Spittle insects live in masses of froth which they whip up on plant stems. The dromiads cut out pieces of sponge which they hold over their backs and are thus concealed. Caddis-fly larvae live in portable or attached tubes which they make by spinning threads and fastening various materials together (Wesenberg-Lund 1911). Hermit crabs commonly live in snail shells but may inhabit holes in corals or sponges. Shipworms and some crustaceans make holes in piles and thus destroy much property; timbers on land are also seriously injured by boring insects. Certain sea urchins and

clams even bore into rock. Many animals dig burrows in the soil. Gophers have elaborate tunnels with compartments for the storage of food, the burying of excreta, and other purposes. Many marine worms line their burrows with secretions from their own bodies and often include foreign materials. The tubes of some of these worms have collapsible ends which are closed by valves to prevent the entrance of enemies; other tubes close up by having the ends roll like a young fern frond. The ant lion has a burrow at the bottom of a sand pit, and every windy day is one of hard labor, for sand must be thrown out of the pit continually. Among insects there are many expert home builders—workers with silk, mud, paper, and other materials (Sjustedt 1916). A larva of Bucculatrix when ready to pupate not only spins a cocoon but surrounds it with a stockade of spikes. Birds exhibit a great variety of homes: that of the magpie is roofed over, and the doorway surrounded by thorns; that of the oriole, pendant and safe at the tip of a branch; that of the flamingo, a mud tower in a muddy flat; etc. Birds have two types of young: (1) *altricial,* which are usually reared in safe places, are carefully cared for by their parents, and show no fear for some time after hatching; (2) *precocial,* which show fear soon after leaving the egg and soon shift for themselves. Beavers prepare for a home by damming a stream. The resulting pond furnishes a place for a lodge and for the storage of winter food; it also is a highway which remains passable throughout the winter and gives opportunity for a quick escape from an enemy or for the transportation of materials under the ice.

Protective Behavior.—Holmes (1922) has given a tentative classification of the forms of behavior used by animals for self-protection. He makes two subdivisions: escape and defense, and subdivides the latter into passive and active. Passive defensive behavior includes such measures as closing, rolling up, erecting spines, and emitting odors; active measures employed are biting, clawing, kicking, stinging, hunting for parasites, etc.

Defenses within Animals.—Animals have certain inherent defenses within their bodies. Injuries are repaired to a greater or lesser extent. Antitoxins, phagocytes, or other bodies neutralize or destroy substances that enter the body of an animal and threaten to do it injury. Different species of animals show

varying degrees of resistance to diseases and poisons. Poisonous animals are usually immune to their own venoms, and many animals have natural or acquired immunity to particular poisons.

BEHAVIOR

Reactions.—Interaction with environment is a fundamental property of protoplasm. The behavior of animals consists of movements that cause rearrangement of parts or of whole animals so as to assume different positions in relation to the environment. The most common cause of reaction is a stimulus, or change in the environment, though some responses are brought

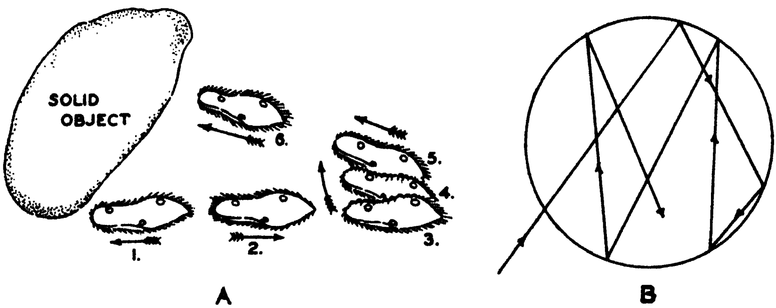


FIG. 28.—Reactions of paramecium. *A*, avoiding reaction when striking an object; numbers indicate successive positions of body; *B*, path of an individual "trapped" in an area that has a slightly acid reaction. (*After Jennings* 1906.)

about by stimulating changes within the animal itself. Reactions are fundamentally regulatory, or adaptive, in that they usually tend to make an animal continue to exist, but they are not necessarily performed in the best possible manner, and sometimes they may actually injure the animal that performs them. Animals with simple organizations are usually able to perform only a few rather stereotyped reactions in response to stimuli; those with specialized nervous systems are able to exercise more or less choice in the time, degree, and nature of their responses. More specialized animals also react more and more to representative stimuli, not for the actual effect that the stimulus may produce but as a sign of the order of events that experience has shown such a stimulus to presage. It might be expected that, if an organism was subjected to the same type of stimulus on two different occasions, its behavior would be the same. Although this holds true in general, it is not always so. The physiological state

of an animal varies and causes an animal to respond now in one way and now in another. The more complicated the mechanism in an animal's body the more possibilities of response it has. A paramecium swims ahead until it encounters a stimulus that causes it to swing about or swim backward or stop. Encountering hundreds of stimuli, it has less than a dozen methods of response. On the other hand, a rabbit that is resting under cover and hears a twig snap has many possibilities of response —it may remain motionless; bound away on a tortuous course, astutely "doubling" to throw off a pursuer; stand up and look for the cause of the sound; or perform countless other acts. Acts that give pleasure or satisfaction or cause an animal better to continue to exist are apt to be repeated, and habits of activity are thus formed; acts that lead to discomfort, pain, or injury are apt to be avoided, and habits of inhibition are initiated. All animals are able to profit by experience more or less. Intelligence, which is the logical outcome of the specialization of such ability, is not the ability to form associations but a high degree of ability to make profitable use of associations that are already formed. Learning is not something new but the facilitation through repetition of fundamental movements and activities.

Behavior and Choice of Habitat.—The behavior of animals often accounts for their distribution in the environment. Shelford (1914) made careful comparisons of the modes of reaction between animals in pools and rapids. He found that there was general agreement among the animals in each habitat. Animals by their behavior tend to find the environment that is best suited to their peculiar types of activities. Kennedy (1925) describes a dragonfly and a May fly "in which a reversal of one or more of the tropisms normal to other species of the same genus has permitted the entrance of these reversed species into environments not open to normal members of the genus." An alpine dragonfly hunts in cold strata of air, often high above the earth, emerges from its nymphal skin in bright sunlight, not at night, and thus is able to live at high altitudes. A May fly that lives in mountain torrents differs from other species in that it rests as an adult in lighted areas and after mating oviposits in shaded torrents. It is thus able to live in a habitat that is "ecologically outside the usual range of its genus."

Behavior of Sessile and Motile Animals.—Probably the most fundamental distinction in behavior is between that of sessile and motile animals. The former tend toward radial symmetry, and it is undoubtedly advantageous for a sessile animal to be able to receive stimuli with equal facility from all directions. Radial symmetry from a psychological point of view is inherently diffuse and unprogressive because different radial axes of the body are more or less of equal importance, and it is, therefore, difficult to have great centralization in control. The animal remains a "republic of reflexes." Animals that move about freely are usually bilaterally symmetrical and have a tendency toward cephalization. Control becomes more and more delegated to the central nervous system, which in the most specialized types exercises nearly absolute authority and is finally able to think of many expedients for adapting various means to particular ends.

Adaptability of Behavior.—For movements to be directed with adaptive relation to the environment, stimuli must be coming to an animal from the outside. A complete living mechanism, if supplied with adequate energy, may give an adaptive, orderly response to such stimuli. Protozoans select proper food from a varied assortment of materials in the environment. A young silversides minnow avoids all large objects, hence spends its youth in open water far from shore and thus generally avoids large predaceous fishes. Animals receive stimuli from their environment and generally respond so that they may continue their activities, but different animals in the same environment do not necessarily respond to the same stimuli. This is where the remarkable adaptiveness of animals is most apparent. Different species are suited by hereditary qualities to receive particular stimuli, and individuals of the same species form various habits of reacting on account of peculiarities in receiving organs or differences in past relations with environment (experience). Emphasis is placed now on impulses initiated by a receptor for one type of stimulus and now on those from another. A bullhead feeds at night, largely through stimuli received by smell, taste, and touch organs in its nostrils and on its barbels. The stickleback feeds by day, depending on stimuli received through its eyes. It chases and tentatively takes into its mouth every bubble or other small object that moves. A dog's world is largely a smell-

ing and seeing world; a man's world is more a seeing and hearing world. Though most animals can perceive a variety of stimuli, each species and individual usually depend primarily on those of one or of a few kinds in making adjustments in order to fit in with changes in the environment.

Law of Parsimony.—Students of animal behavior have, since about 1880, gradually discarded older, rather anthropomorphic explanations for the behavior of animals, and terminology has changed accordingly. The Law of Parsimony has been generally accepted by scientists. This asserts that scientific procedure demands that the simplest explanation that is compatible with observed facts must be accepted. So, when a moth flies toward a light, one no longer says that the insect loves the light, or is photophilic, but that it is positively phototactic, *i.e.*, that it moves toward a source of light without any implication as to what its feelings may be. Such noncommital terminology is now generally used. Animals that turn toward or away from the sources of stimuli are said to show positive or negative tropisms. The term "tropism" in this sense is purely descriptive. It means merely that an animal turns and orients its body in relation to a stimulus. If an animal becomes active after stimulation without orientation, it shows kinesis (photokinesis, thermokinesis, etc.). If an animal orients and *moves* toward or away from a stimulus it is said to show a positive or negative "taxis" (rheotaxis, phototaxis, geotaxis, etc.). Furthermore, it has come to be recognized that, though an animal may be able to perceive and respond to the same types of stimuli as a man does, its sensations may be quite different in quality. For example, if a shrimp comes to rest on greenish seaweed which matches its own color as seen by the human eye, an observer is not justified in assuming that the shrimp loves green or that green pleases it or that it knows that the background makes it inconspicuous or that it sees a color green such as the human eye perceives. The crustacean may be responding to reflected light of particular wave lengths, intensity, form, pattern, or some other quality in the stimulating object. Students of behavior have gradually become increasingly cautious in their statements concerning observed phenomena.

Responses to Touch.—Touch stimuli play a leading role in the lives of many animals. Whether a hydroid stem develops

into a stolon or a hydranth depends, in some cases, on whether or not it encounters a solid object. The ichneumon Thalessa is able to bore through a considerable thickness of solid wood with its ovipositor and reach the larva of its host Tremex. An earthworm is said to be stereotropic because it is usually restlessly active unless its body is in contact with the walls of its burrow or with some similar surface. Stereotropism, geotropism, and to some extent rheotropism are all responses called forth by pressure against objects. Lyon (1904) in his admirable paper on rheotropism shows that so-called rheotropic responses are brought about by optical or tactile stimuli. Rheotropism is a form of compensatory motion which tends to keep animals in the same spatial relation to certain objects in their environment.

Responses to Sounds.—Auditory stimuli produce pressure on appropriate receptors, but stimulation differs from touch in that it is concerned with vibrations in ponderable media. Sounds are of value to animals: as warnings; as call notes, particularly as signals during mating and for keeping groups together; and as a medium for language expression. Hartridge (1920) has advanced the view that bats are able to fly about in total darkness by emitting high sounds which are reflected back to their ears from obstructions, which thus may be avoided.

Responses to Thermal Changes.—Temperature is effective for many animals as a limiting environmental factor through its influence on the rate of metabolism, but differences in temperature are also received as stimuli. Cases are rare where temperature serves as a directive stimulus, however. Animals tend to rest near their optimum in cool or warm places but usually do not go directly toward or away from such situations unless they have a high order of psychic development (Hecht 1930, Nieschulz 1933).

Responses to Chemicals.—Chemical substances are often important stimuli. Animals use tastes and odors for judging the suitability of foods; for the recognition of particular individuals, foods, places for depositing eggs, etc.; for keeping predaceous animals away; and for other purposes. The life of a honeybee is dominated by odors, and each individual produces odors that are characteristic of its hive and sex. The primary basis for the social life of bees, ants, and certain other insects is in the odor sense. A filtered solution from a Paramecium

culture will cause a Didinium to emerge from its cyst and take up an active life, though it cannot find sustenance, for its food consists of living protozoans. There has been some discussion as to whether or not aquatic animals have distinct senses of taste and smell. Recent experiments demonstrate that smell serves fishes, as it does land vertebrates, for the perception of very dilute solutions and that taste is used for the discrimination of those of greater strengths.

Responses to Light.—Light may be a nondirective stimulus, merely exciting an animal to activity, or cause animals to assume definite orientation with relation to it and perhaps also cause them to move directly toward or away from it. The skin of many animals is sensitive to light, but many others have special pigmented areas and eyes of various sorts for light perception. The simpler eyes merely allow an animal to perceive with more or less accuracy the direction from which light comes, but the more complicated types enable animals to perceive images and distinguish colors. The camera eyes of vertebrates give very good images of objects, but the compound eyes of arthropods are probably superior to them as organs for perceiving motion in the environment. It was long a dogma that Paramecium is absolutely insensitive to light, but recent experiments show that if this protozoan is in motion and the light intensity is suddenly increased, the rate of locomotion is also increased. Water mites show similar correlations between speed of locomotion and light intensity (Welsh 1932). Some animals are very sensitive to changes in light intensity. Thyone and Hydroides will contract at once if a glass rod is passed between them and a window. The moth larva that lives on coffee leaves is apparently sensitive to the absolute amount of light. It never comes out into the direct sunlight but frequents the upper surfaces of leaves on cloudy days, on bright days being found underneath.

Most animals that commonly respond to light as such are stimulated, as far as quick reactions are concerned, by the time rate of change in the intensity, but the absolute amount of light is chiefly responsible for the periodic activities of animals that are markedly diurnal or nocturnal. For example, if the amount of light is decreased very slowly Hydroides does not withdraw into its tube, but if the decrease is rapid it snaps back at once; chickens usually will go to roost when the light is decreased during

an eclipse. Changes in the amount of light serve as signs for many animals and influence behavior accordingly. A hermit crab avoids shadows as indications of passing enemies; leeches wave their bodies or swim in the direction of movement of shadows and thus often gain attachment to hosts. There is a general migration of plankton animals up and down with the daily changes from dark to light, but all species do not rise or descend when the light has reached the same degree of intensity.

Animals that can make use of light to perceive images and that can distinguish different wave lengths have unusual advantages in adjusting themselves in the environment. A jumping spider or a tree frog can judge distances with great accuracy and is thus able to leap on its prey with certainty. An animal like a vulture which habitually soars high above the earth must depend for a livelihood chiefly on its eyes. The ability of the honeybee to discriminate colors and patterns is of great value in seeking food in flowers. The remarkable resemblances of many animals to the colors and patterns in their environment are to be taken as evidence of the sharp vision of predators.

Homing Behavior.—Animals often show place association, particularly those that have more or less permanent homes. Limpets rest on rocks along the shore of the ocean (Abe 1935). They remain in one spot so long that they sometimes wear little scars and if moved a few inches away will return. Arey and Crozier (1921) studied the homing of Onchidium, a pulmonate that lives in colonies of about a dozen individuals in crevices along the shores of Bermuda. Each snail leaves its home crevice for about an hour each day to feed. It returns to its own crevice and cannot be induced to enter any other. Arey and Crozier believe that Onchidium recognizes its home by "contact odor," and their observations give no evidence of associative memory. Crabs that live in burrows and similar habitations often show pronounced homing habits. In the Philippines the writer once moved a fiddler about 30 ft. from its burrow, and the crab returned to the same spot after 28 days. The old burrow had long been filled up by the tides, but the little crab dug a new one beside the stake that had been set to mark the place. Many insects resort to particular places. Certain butterflies have resting spots, and they attempt to dislodge any intruder that may have squatted on the property during their absence. Bees

wasps, and ants have nests that are the center of their activities. There has been considerable controversy as to which senses are most used by ants and other insects with pronounced homing habits. Wasps and bees depend much upon landmarks. According to Pieron (1913), different kinds of ants return home by the use of different senses, Formica and Camponotus depending mostly on landmarks, Lazius using odor trails, and Messor utilizing "muscular memory." Various fishes, amphibians, birds, and mammals have homing habits. It has been determined by banding birds that they return to the same spot to nest year after year; even the penguins in the Antarctic resort to the same rookeries. Noddy terns are able to return quickly over the open ocean for distances of 800 to 1,000 miles, just how is uncertain (Watson and Lashley 1915, Watson 1920). It is known that homing pigeons can return from greater distances if they are allowed to observe the route over which they are taken from the home cote.

Tropisms, Habits, Instincts.—Protozoans and many other animals respond to stimuli largely by tropisms, which are repeated over and over without much modification whenever the appropriate stimulus is repeated. A Paramecium that is dropped into a toxic solution keeps on giving "avoiding reactions" until it dies; a moth will fly persistently against a lamp, showing maladaptation of a tropism that under normal conditions would be generally useful. *Tropisms* are for whole animals somewhat like the reflexes of parts of animals. If acts are repeated they are usually performed more readily and thus grow into *habits*, which are useful because they enable an animal to save some of the time, attention, and labor that is necessary without learning. Memory is important in the relations of animals with environment, enabling them more readily to avoid dangers that are encountered repeatedly and to find food more easily through experience. *Instincts* are complicated acts which are characteristic for each species and which an animal is able to execute with some degree of perfection without learning. They have been defined as "inherited," or "racial," habits, the supposition being that they have been fixed by repetition during phylogeny and are now a part of the specific inheritance of each species. Instincts concerned with the procuring of food, locomotion, defense, escape, homing, and social life are usually more or less continuously

active; those concerned with reproduction are often cyclical or periodic, like those for migrating, mating, nesting, and incubating; some instincts are transitory and usually appear irregularly at certain periods in the life cycle, like play and the climbing period of certain young birds (Herrick 1920).

Levels of Response.—Animals that have only a few simple reflexes, tropisms, and instincts must lead very simple lives and have limited relations with environment. They spend their time seeking food, eating, digesting, avoiding danger, resting. Animals that have attained enough complexity, so that they do not have to respond to every stimulus but exercise some degree of choice in their methods of response, can conserve energy and have more leisure for practice and hence may attain perfection in complicated acts. Animals that can reason may go beyond the reflex and instinctive endowment that they inherited. They invent new methods of procedure and have leisure for the intellectual enjoyment of living, recalling the past and anticipating the future for pleasure, playing for mere pleasure and not only because the skill attained gives better chance of survival. They may even acquire many purely mental standards for living which have no reasonable basis but are dependent on custom. All animals show more or less ability to profit by experience, or to learn to adjust themselves to the environment in which they live. Certain of the processes involved in such adjustments are similar from protozoans to mammals (Shelford 1918*a*). Learning processes are limited by inherent, inherited structural and physiological qualities. A metazoan with an epicritic nervous system and highly efficient sense organs can in some respects adjust itself to environment better than a simple protozoan. It can even think of means of changing environment to suit its own system of activities. From one point of view "behavior is the result of external necessity, rather than internal organization" (Anderson 1936). Various theories of learning have been supported by students of animal psychology. Among these Warden, Jenkins, and Warner (1935) discuss four types: (1) mentalistic theories, in which conscious selection is stressed; (2) algedonic theories, in which selection is ascribed to physiological states resulting from pleasant and disagreeable sensations; (3) practice theories, in which selection of acts depends on frequency, recency, and intensity factors in a stimulus situation;

and (4) dynamic theories, in which selection is held to be due to such internal factors as are called drive, determining-tendency, or action-tendency, and these depend on inherent constitution and past experience. Melrose (1921) arranges types of animal learning in six levels which include fixation, spacial accommodation, choice, association, conception, and judgment. Intelligence is capacity to adjust thinking consciously to new requirements. Every situation in a complex environment is more or less old and new. The degree or amount of intelligence is determined by "native capacity or neural complexity" (Carroll 1928). Social animals, such as men, have three types of inherent abilities which have been classified as social, mechanical, and symbolic. One individual mixes with his fellows and is generally successful in his relations with them; another may be a genius with tools and machinery; and a third cannot make his clock run or get along with his neighbors but perhaps has remarkable ability to solve abstruse problems in philosophy or mathematics. A particular type of personality may make an individual successful or unsuccessful in the environment in which he lives. Personality depends on the integration of various levels of activities: physical, chemical, biochemical, physiological, mental, and instinctive (Paton 1921). Behavior is a means for adjustment to environment. As perceptive organs, nervous systems, and effectors have grown more complex and efficient, animals have been able gradually to progress from the general use of contact relations to distance perception and the exercise of a high degree of judgment. Especially on land, animals have become quick, swift in locomotion, and more or less thoughtful. They recognize objects from considerable distances. Thus they are capable in avoiding dangers and finding food.

CHAPTER V

EVOLUTION, CHOROLOGY, SUCCESSION, CLIMAXES

EVOLUTION

Animal and Environment.—An animal cannot exist without environment. "The organism and the environment interpenetrate one another all through" (Sumner 1921). Bather (1920) remarks:

For the evolutionary biologist a species contains in itself and its environment the possibility of producing its successor. The words "its environment" are necessary because an organism cannot be conceived apart from its environment.

Adaptation to Environment.—Paleontologists agree that progressive evolutionary changes in the past have generally been correlated with striking environmental changes and that wide diversity of particular types came about during prolonged periods of comparative stability.

The great upward steps in evolution are primarily determined by environmental changes which operate to diminish the quantity of life and work toward the extinction of ancient types. On the other hand, in the splitting of a family into various subfamilies, genera, and species, the leading rôle would seem to be taken by a tendency toward organic change, the environment remaining in the meantime nearly constant (Barrell 1917).

According to Barrell's view, the great steps in evolution are not a consequence of life but are forced by climatic change. The species that have persisted unchanged during the longest periods of time have been those that were in most perfect adjustment with the environment. During periods of environmental stress and change, new types appeared; and during the favorable conditions afforded by long periods of stable environment, competition and perhaps other factors caused the differentiation of established types. There is no question that, in a general way, evolutionary

transformations in animals have been correlated with environmental changes.

Limits to Adjustment.—In relation to powers of adjustment, animals have two types of characters: (1) those that may change during the life of an individual and (2) those that may be modified only after long periods of time. In order that evolution may take place, it is necessary that species change. It is, therefore, necessary that modifications of systems of activities be transmitted in some way from one generation to another. The great questions of evolution at the present time are: (1) What causes animals to vary? (2) How do modified characters become a part of the system of activities that passes on from one generation of animals to the next? For an ecologist, the important question is, How do animals become adapted?

Animals continually become adjusted to minor changes in environment. The amount of perspiration given off from a man's body is correlated with variations in air temperature; the lengths of the terminal spine and the helmet on the body of the little crustacean *Daphnia longispina* are correlated with the temperature and viscosity of the water in which the animal lives and are also markedly influenced by the character of available food (Woltereck 1909); drug addicts become tolerant to doses of poisons that would be fatal to those unaccustomed to the use of drugs; a person who has survived an attack of smallpox is immune to the disease. Everywhere that animals live there are instances of adjustment to environment. But adjustments made during the life of an individual are rarely, if ever, transmitted. The children of a drug addict do not have unusual toleration for drugs, and persons who have had smallpox do not transmit immunity to their offspring. Although every animal system of activities is free to make many minor adjustments, the main features and limitations are hereditary. Even the selection of peculiarly "adapted" individuals through a number of generations does not essentially change the hereditary pattern that is characteristic of each species. The stock reverts to the original conditions as soon as the selection of peculiar individuals ceases, unless a mutant, or an animal that has already acquired a new range of variation, is accidentally selected.

The details of animal response are free from hereditary restraint and depend more or less upon the varying physiological states of

the animal, but the main features of behavior cannot be changed from the hereditary species pattern. The range of activities is hereditary. The difference between readily adaptable and comparatively stable adaptations is apparently merely one of degree, but the latter to some extent rather inflexibly hold species in the parental groove. Adaptation does not mean that an animal by striving to reach a certain state can do so but that it has certain given characteristics that happen to fit the environment in which it lives. It may have certain characteristics that do not fit the environment, but it can continue to live if these have no vital bearing on the adjustment of its activities. "A species perfectly adapted to its environment may be destroyed by a change in the latter if no hereditary variability is available in the hour of need" (Dobzhansky 1937).

Ecologically, limitations can be seen in the powers that animals have of adjusting themselves to changes in the environment. Some animals, like *Daphnia longispina*, assume different forms that appear better to correlate their activities with various environmental conditions. Others show striking instances of adjustments to regularly recurring states in the environment. there are adaptations to daily, monthly, and seasonal cycles. There are some orderly processes, however, to which animals are apparently unable to adjust themselves. For example, when a pond is physiographically young, it furnishes a habitat for many species of animals. As mud and aquatic vegetation accumulate and fill the pond, there is, after many years, a succession of species, and in its old age the pond has a different fauna from that present in the beginning. Shelford (1911) studied the fishes in ponds along the shore of Lake Michigan. He found that the young ponds contained several species of sunfishes but that in the older ponds such fishes were entirely absent and the dominant species were bullheads and mud minnows. In this instance the members of the sunfish family doubtless possessed the usual powers of adjustment, but their hereditary patterns made them unable to go far enough to keep pace with the physiographic changes; hence they were succeeded by other species with different hereditary patterns that permitted them to flourish under the new conditions.

Variation and Environment.—Some evolutionists doubt if any adjustment to environment that is modifiable during the life of an individual can exert an influence on hereditary qualities.

They hold that animals are produced with a certain range of adjustment that cannot be changed by any factor of the environment. From this point of view adaptation to environment is, in a sense, accidental. Characteristics are present; if they fit the environment, an animal may exist; if they do not, the animal cannot exist. Heredity gives ability; environment furnishes opportunity (Pearse 1932). Such hereditary qualities as sex characters depend for their expression on environment, hormones, and gene characters (Witschi 1936). All apparent characteristics are hereditary, and all are environmental (Jennings 1924, 1935). With this point of view in mind it may be well to examine some of the views concerning the causes and factors of evolution, with particular reference to their applications to ecology.

Variation and Evolution.—To understand evolution, it is essential to account for genotypic variations in animals, and this has not as yet been done satisfactorily. It is known that each species consists of a mixture of diverse strains which breed reasonably true to type if selected and kept segregated. Such selection of strains has been made among protozoans by Jennings (1920) and among domestic animals by many persons. Among many animals conjugation changes the range of variation, either by the recombination of characters already present or through the intensification or weakening of characters in some other way. Dedifferentiation in one direction apparently precludes return to a generalized condition, and evolution is, therefore, orthogenetic. The specialized types of one epoch do not produce the dominants of the next; dominant forms usually spring from labile stocks. Evolution is both continuous and discontinuous (Sumner 1927). Genes show quantitative differences; a species is the result of a series of mutations, not one. It is known that parts developed to an extraordinary degree are apt to be more variable than those that are not. It is also recognized that wide-ranging species are ordinarily more variable than those with restricted ranges. But all these and other known facts do not solve the problems of variation. Hereditary changes are produced, and no one knows exactly how or why.

Transmission of Acquired Characters.—Though there is little or no *evidence* that adaptive characteristics acquired during the life of an individual are transmitted to the next generation, Semon (1904) insists that heredity is racial memory; Davenport

(1908) believes that individual attunement initiates racial attunement; and Child (1915), that an animal's threshold of stimulation can be gradually increased and that this condition may be inherited. Jennings (1911) states that:

> The gradual formation of developmental habits seems to be the only form of the idea of the inheritance of acquired characters that is not opposed by any of the experimental facts, that helps us to understand why so many characters are not inherited—since they are not produced by the developmental processes of the organism—that fits all the recent cases that give positive evidence for the inheritance of acquired characters, and that is based on law actually known to hold for those organic processes that are most favorable for study with relation to such laws.

Until there is more evidence, it must be held that, though hereditary characters must change if evolution is to take place, environment apparently has little importance as a direct causative agent in producing such changes. Shull (1917, 1936) expresses the opinion of many modern biologists when he says that evolution is due to chemical changes in chromosomes and that the inheritance of such changes is "usually, if not always, independent of the environment." Noble (1930) makes similar statements. But there are still those who believe in the direct effects of environment on genetic constitution (McDougall 1938).

Selection and Environment.—After species change, and new hereditary characters have actually come into existence, natural selection appears to be the most important agency for preserving such new ranges of adjustment. It is often difficult to determine what is beneficial or injurious. The world maintains a continual dynamic balance in which the dying out of a species at times may be useful for the continued maintenance of a larger ecological unit (Peter 1935). Davenport (1903) has pointed out the importance of the environment in selection and advanced a "theory of segregation in the fittest environment" which supplements Darwin's natural selection theory. According to his view, unadaptive variations may become adaptive, "if they can find their proper place in nature." "Suitable" structures may appear before they find proper environments. This has often been called preadaptation (Goldschmidt 1933).

Environment and Evolution.—Altogether, environment has played an important role in evolution. It has furnished a

culture medium for the incubation of variations, has limited the line of development that could take place, and has even exercised control over the rate and extent of evolutionary changes. There has, however, been no general conformity when diverse animals made adjustments toward a condition of stability in a particular environment. Environment does not always eliminate unfit, or maladapted, individuals; it does tend to stabilize and conserve certain stocks. Animals have attained similar ends by very diverse means; structure and classification are not closely related to habitat. At times slight structural differences between species are correlated with differences in habits; at other times species having almost identical structural patterns show radically different responses to environment. These facts indicate that environmental variations are not the direct cause of evolutionary variations. Variation does not match environment closely enough, it makes too many detours into blind alleys. Perhaps the evolution of habits has usually preceded the evolution of structures. Robertson (1906) believes that new species arise through an overpopulated condition, which forces certain individuals to take on new ranges of adjustment to the environment. Natural selection then operates in favor of individuals that change their habits. If an epidemic occurs when a region is overpopulated, a group of peculiar, resistant individuals may be left. These may incidentally carry over so-called indifferent, or useless, as well as adaptive, characters and thus lead to a new species. Robertson claims that the ecological basis for a hereditary morphological change is in the taking on of a new use for a structure. The evidence to support this rather attractive view is still to be found.

Evolution and Energy.—Osborn (1917) has advanced an "energy conception of life" which depends on "action and interaction," and he claims that organisms have developed according to law rather than chance. According to his view there has been, since life began, a continual interaction between environment, organism, germ plasm, and life environment (that made up of living organisms). His discussion is of value in directing attention to the fact that organisms have never been separated from environment but it does not furnish the needed *evidence* on the causes of variation. Osborn (1934) also stresses the fact that there are two processes concerned in evolution: one

"continuous, gradual, direct, definite in the direction of future adaptation"; the other sudden and mutational. Both become part of the hereditary equipment of an organism. They constitute his creative principle, aristogenesis, for new species. Kennedy (1928) has pointed out that primitive insects in general have slow metabolic rates and live in habitats where least energy is available, whereas specialized insects live rapidly in situations where there is much available energy. Evolution has probably been most rapid in the tropics, where high temperatures permit generations to pass quickly, as compared with cooler climates (Worthington 1937).

ISOLATION

Geographic Isolation.—There is no doubt that the separation of groups of animals on particular areas of the earth has been an important factor in the formation of new species. The faunas of remote oceanic islands give striking evidence of the effects of isolation. Among certain of them the presence of wingless insects and birds furnishes remarkable examples of adaptation to peculiar environmental conditions. Such a learned and thoughtful zoologist as the late Dr. Ortmann (1912) said "it is absolutely unthinkable that two species may be derived from one ancestral species without the action of isolation." He also pointed out that the fact that various species or subspecies together occupy a continuous area, or even overlap, does not prevent isolation. Distribution may be continuous, but continuity of biotic conditions over a large area never is. Ortmann stressed the action of four evolutionary factors, variation, inheritance, selection, and separation. A "biotic area" is perhaps a more significant unit in animal distribution than a "life zone" (Dice 1922). Long periods of time appear to be required for the evolution of races or species that closely fit different but contiguous environments. After many generations mice transferred to different climates in California showed no significant change (Sumner 1917, 1924). The snails in the Society Islands after many years showed changes in distribution, but conditions of environment did not seem to have been directly related to them (Crampton 1925).

Biotic Isolation.—Isolation does not always result from the segregation of animals in separate geographic areas. Animals may live intermingled on a single area and yet be prevented from

having relations with each other. At the mouths of the rivers in Siam and India several species of gobies skip about together on the tidal mud flats; yet they occupy separate ecological niches because they eat different foods, are infested by different parasites, have different modes of breeding, and show other specificities (Hora 1936, Pearse 1933). The herring, *Clupea harengus*, consists of two races which spawn in spring or autumn (Lissner 1934). Certain insects escape competition by what Kennedy (1925) calls "reversed behavior," so that their activities occur at different times or places from related species. Numerous instances are known among insects in which varieties of a single species are separated from relations with each other because each shows preferences for certain foods, for both sustenance and oviposition (Thorpe 1931*a*). Three races of the cricket, *Nemobius fasciatus*, have been described that sing quite different songs and occupy different habitats. If these insects did not sing it is doubtful if the different types would have been detected. "All evidence so far leads one to conclude that the three races of *Nemobius fasciatus* are more distinct physiologically than morphologically, and that they seldom if ever interbreed under natural conditions" (Fulton 1933). Races may be separated by food preferences and breeding habits, disinclination for crossbreeding, hybrid sterility, etc. In other words, isolation may be due to factors that may be called geographical, sexual, psychological, ecological, mechanical, etc. (Dobzhansky 1937). There are various types of variation; some are plastic and some are inflexible (Harms 1935). The late E. P. Lyon once suggested that biologists talk too much about variation and neglect similarity. He stressed the wonder of the fact that any two protoplasmic systems could be as much alike as some are. In certain habitats groups of fit, or adapted, individuals are evolved, and biotic isolation appears to be an important factor in this process.

Ecological Segregation.—In evolution both organisms and environments select (Davenport 1903). Animals tend to spread into, and if possible occupy, all available habitats; they try all possibilities and select what is favorable. Environment selects by fostering or destroying animals that do or do not fit. Animals tend to segregate, or isolate themselves, into particular habitats. They thus avoid competition by taking advantage of unoccupied ecological niches. They may do this by taking advantage of new

food supplies, unoccupied breeding places, and other unexploited resources or refuges. Most animals cannot digest such foods as wood and wool, but a few have found their niche by gaining ability to do so. When a group of individuals in any species takes on a new mode of life, it may be beginning a new species (Robertson 1906, Pearse 1934). Biotic isolation leads to new ranges of toleration, to ecological segregation, and thus contributes to the formation of new species. Competition will be discussed in Chapter VII.

DISTRIBUTIONAL MOVEMENTS

Types of Movements.—Heape (1931) has proposed the following terms and definitions: *emigration*, movement of animals from one locality to another without returning; *migration*, more or less periodic movements of animals between two localities; *nomadism*, wandering of animals over a restricted area or over any areas; *dispersal*, more or less passive carrying of animals from one locality to another; and *diffusion*, spreading of animals beyond an original area occupied, without leaving it. All these terms seem to be well chosen, except the last, which generally has been used in a quite different sense by scientists. The writer therefore adopts Heape's terms but substitutes *spreading* for diffusion.

Emigration.—There are many known instances of great movements of animals away from areas that they have occupied for generations. Notable among these are those of lemming from the highlands of Scandinavia over surrounding territory, even ending in some instances in the swimming of the excited, persistent little rodents into the sea, where they perish. Emigrations of spring buck in Africa, moose in Canada, rats in various localities, wolves from Canada to the United States, sand grouse from Africa into Europe, waxwings, crossbills, rough-legged buzzards, rooks, crocodiles, tile fishes, halibut, and other vertebrates have been observed (Heape 1931). Mass emigrations are also well known among invertebrates. Movements by myriapods (Thuringer 1934), termites, dragonflies, butterflies, moths, and hymenopterans furnish good examples. Among vertebrates emigrations are generally brought about by lack of food following periods of rapid reproduction, so that an area becomes overpopulated. Among invertebrates food shortage is not so clearly concerned, but emigrations occur after periods of rapid multiplication. Emigrations appear to be more or less blind movements away

from starvation conditions and overcrowding. Routes often are not wisely chosen, and most emigrants die without gaining a foothold in new territory. Some emigrations, however, are successful. Moose move to new grazing areas at intervals. Apparently this is because the quality of forage in areas long used deteriorates. New, unoccupied areas when invaded apparently give moose renewed vigor for several years. Ekman (1920)



FIG. 29.—Sooty and noddy terns on Bird Key, Dry Tortugas, Fla.

believes lemming move mostly westward during their migrations in Scandinavia because they occupied lowland areas there during glacial and interglacial times and now revert to their old feeding grounds during periods of stress. After great climatic changes, such as those which followed the northward movement of ice after the Glacial Epoch, there were very extensive emigrations. Animals moved in great bands across continents and occupied new areas (Adams 1905). Gregarious or colonial animals, such as rooks and bees, when a colony becomes large and thus perhaps makes foraging more difficult, split off groups of emigrants which establish themselves elsewhere.

Migration.—Migrations are discussed in Chapter VI (page 183).

Nomadism.—Herds of deer, packs of wolves, and many other groups of animals wander about continually in search of food and other essentials for life, in some cases over rather definite routes and in others anywhere over suitable areas. Both grazing animals and insectivorous birds often hunt in flocks made up of different species. This makes observation of and escape from enemies easier for animals preyed upon and helps predaceous animals capture food. A hundred pairs of eyes are more likely to observe a lurking enemy than one; a fleeing insect is easily surrounded and caught by a group but may escape from a single predator. Sometimes groups of nomads wander off areas that they originally occupied and, finding suitable habitats elsewhere, become emigrants to a new locality.

Dispersal.—Animals may be transported across stretches of ocean on mats of floating vegetation, logs, or ships. Winds and currents may carry animals long distances. Commensals and parasites ride about with their hosts. Lampreys and remoras attach themselves to the bodies of larger and stronger swimmers than themselves; endoparasites may be introduced into new areas with their host emigrants. Flying birds may carry small animals for long distances among their feathers or between their toes. Along the coast of New Zealand there is an ascidian, *Boltenia pachydermatina* Herdman, which grows in little groups attached to pebbles. As these animals mature they become buoyant, so that the colony and its pebble are lifted off the beaches and carried away by tidal currents (Chilton 1926). Sometimes fishes rain down on land areas from the sky. They are swept out of shallow waters by strong cyclonic winds and transported various distances before they are allowed to fall (Gudger 1929, Hora 1934, 1935). Oceanic islands often show the effects of dispersal. Their faunas may lack whole groups of animals that occur on the nearest continents because they have been populated more or less by accidental arrival of objects brought by currents, winds, etc.

Spreading.—A group of animals that is established in a particular locality tends to spread over adjacent areas when conditions are favorable or become restricted if they are unfavorable. Often ecological succession toward a climax helps to spread certain species (Elton 1927). Near the town of Kodiak, Alaska, the Sitka spruce forest is slowly advancing northward. Griggs (1937) points out that there is "a general belief among botanists . . .

that tree growth is limited by the isotherm of 10°C. (50°F.) for the warmest month. It is interesting to observe that in southwestern Alaska the isotherm stands 250 miles beyond the edge of the forest." The forest there is creeping slowly into the grassland, about one mile per century. As it advances, sylvan animals go along. The activities of man, such as clearing, tillage,

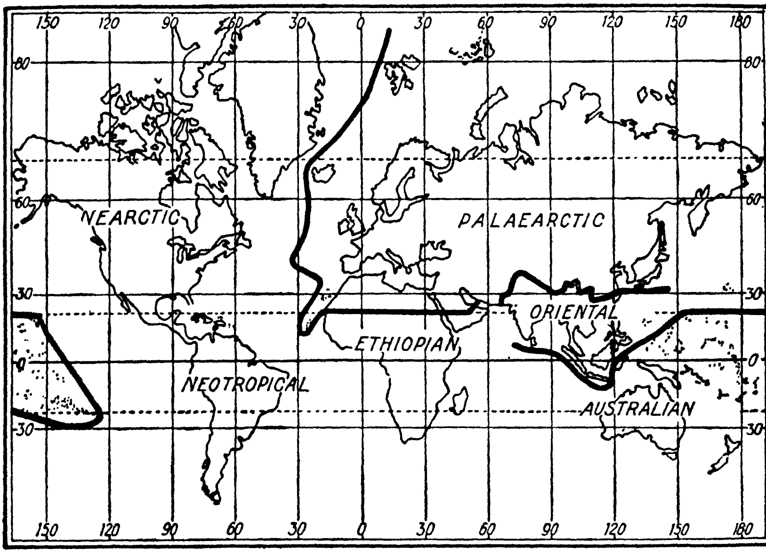


Fig. 30.—Wallace's faunal regions of the world. (*From Chapman* 1931.)

and drainage, cause spreading or restriction of the ranges of certain animals.

ZOOGEOGRAPHY

Habitats on Earth.—The surface of the earth is made up of land and water. The area of the land surface is 28 per cent of that of the earth, and its average height above sea level is about 2,250 ft. The area of the water is 72 per cent, and it has an average depth of 13,860 ft. A priori, one should perhaps expect to find more species of aquatic than of terrestrial animals, and, were it not for the marvelous variety of adjustments that insects have made to various environmental conditions, this expectation would be fulfilled. There is more water to be inhabited than land. Water is a more stable habitat, and paleontological evidence indicates that life existed there first. The early animals

were apparently all marine. If variation in animals is due to variation in environment, then the water should support fewer types of animals because it is, and has been, more stable. Perhaps little variation has permitted more types to occupy the same region of the environment in water. More offshoots of generalized types of animal structure exist in the ocean than elsewhere, however, and some whole groups of animals (like the echinoderms, brachiopods, and cephalopods) have never been able to establish residence in freshwater or on land. Although

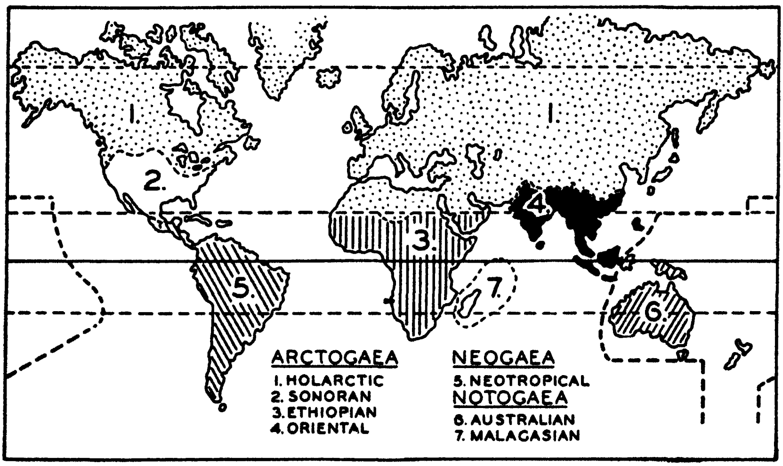


FIG. 31.—Realms and zoogeographic regions of the earth. (*After Newbigin* 1936.)

the ocean remains the home of many established, archaic types, some of the more progressive animals have, during the long periods since life began, emigrated to freshwater and land habitats. Again some of these have emigrated back into aquatic habitats. Freshwater has perhaps received more emigrants from land than from the ocean.

Present Distribution of Land Animals.—Alfred Russel Wallace (1876) may be looked upon as the founder of the modern science of zoogeography. According to the distribution of characteristic animals he divided land areas into six regions: Palaearctic, Nearctic, Neotropical, Ethiopian, Oriental, and Australian (Fig. 30). These have been modified but little by recent chorologists. There has been a general tendency to combine Wallace's first two groups as the Holarctic; a Sonoran Region has been

recognized between the Nearctic and the Neotropical; and Madagascar has been separated from Africa as a Malagasian Region. Newbigin's (1936) classification, with a few representative animals, is as follows (Fig. 31):

Realm	Region
I. ARCTOGAEA	1. *Holarctic:* ungulates (bison, elk), beaver vole, hare, insectivores; no edentates; few or no primates.
	2. *Sonoran:* peccary, armadillo, etc.
	3. *Ethiopian:* (old-) hyrax, lemurs, aard-vark; (new-) ungulates (antelope); no bear, deer, sheep.
	4. *Oriental:* complex; peculiar civets, insectivores, etc.
II. NEOGAEA	5. *Neotropical:* sloths, llama, vicuna, rhea, etc.
III. NOTOGAEA	6. *Australian:* marsupials, duck-bill, moa, etc.
	7. *Malagasian:* lemurs, insectivores, etc.

Both the Ethiopian and the Oriental Regions have remnants of archaic faunas and also have been invaded by more modern animals from the north. This has happened to a lesser extent in South America (Neotropical). The Australian and Malagasian Regions apparently have been isolated for a long time, and today many old groups which have not been superseded by modern animals are still indigenous. Such great regions as those suggested do not have remarkable unity in their faunas. Though each has a characteristic fauna, it is a more or less complex mixture of old, native animals associated with those which have invaded the area now occupied at various times and from various directions. For example, the Oriental Region may be subdivided into a Burma-Malay Section (flying lemur, tapir, etc.) and an Indian Section (sheep, goats, hedgehog, etc.). Tigers have emigrated part way across it from the east; lions, from the west. Its fauna is made up of animals from various sources.

Marine Geographic Regions.—Though regions and barriers are not so clearly defined in the oceans of the earth as on land areas, there are generally recognized districts where characteristic plants and animal communities are found (Ekman 1935). Partially enclosed seas have distinctive faunas (Hubbs 1930). Faunas may be recognized as: Tropical Littoral, Mediterranean-Atlantic, Atlantic-Boreal, North Pacific Temperate, Arctic,

South Atlantic-East Pacific, Indo-West Pacific, Antarctic, Abyssal, and Pelagic. The last differ in warm and cold seas and in deep waters (bathypelagic). Some types of animals in their distribution show bipolarity; *i.e.*, they occur in polar or temperate seas but not in the tropics between. Ekman believes such types probably originated in temperate, rather than equatorial, seas. Some animals that live in the open sea are found along the borders of currents, where food may be abundant (Brooks 1934).

Zoogeography.—Time was when chorologists were satisfied to do nothing but map and group the distribution of animals on the earth, but recently the outlook among zoogeographers has faced more toward the dynamic aspects of the subject. At first animals were sorted into characteristic regions. Then animals were arranged in zones between isothermal lines around the earth (Merriam 1891). Though temperature is still recognized as a primary factor in its influence on animal distribution, such zonal arrangements have met with increasing difficulties (Kendeigh 1932, Shelford 1932), and ecologists have pointed out that natural animal communities do not usually fall into zones. Arrangements according to habitats or biotopes (Hesse, Allee, & Schmidt 1937), biotic areas (Dice 1922, 1923, 1931), or ecological niches (Grinnell 1928, 1935) have been proposed (Fig. 32). Attention has turned from areas and zones to habitats and natural communities. Zoogeography is now ecological as well as statistical (Prenant 1933). Furthermore, it has come to be recognized that the present distribution of animals depends not only on present conditions but on those that obtained in the past. This has led to attempts to correlate present conditions with ancient land bridges, ocean basins, and other extinct barriers or highways (Ortmann 1902; Fig. 33). Hopkins' (1918, 1938) Bioclimatic Law (p. 42) stresses the effects of altitude, latitude, and longitude on the distribution of plants and animals. It is also recognized that Liebig's Law of the Minimum is significant; the factor that varies below an organism's limit of toleration prevents it from becoming established in an area (Shelford 1913). Geographic races have raised difficulties in the study of chorology, and all these have not yet been overcome. Willis (1922) proposed his theory relating to "age and area," *i.e.*, that wide-ranging groups are to be looked upon as older than those found

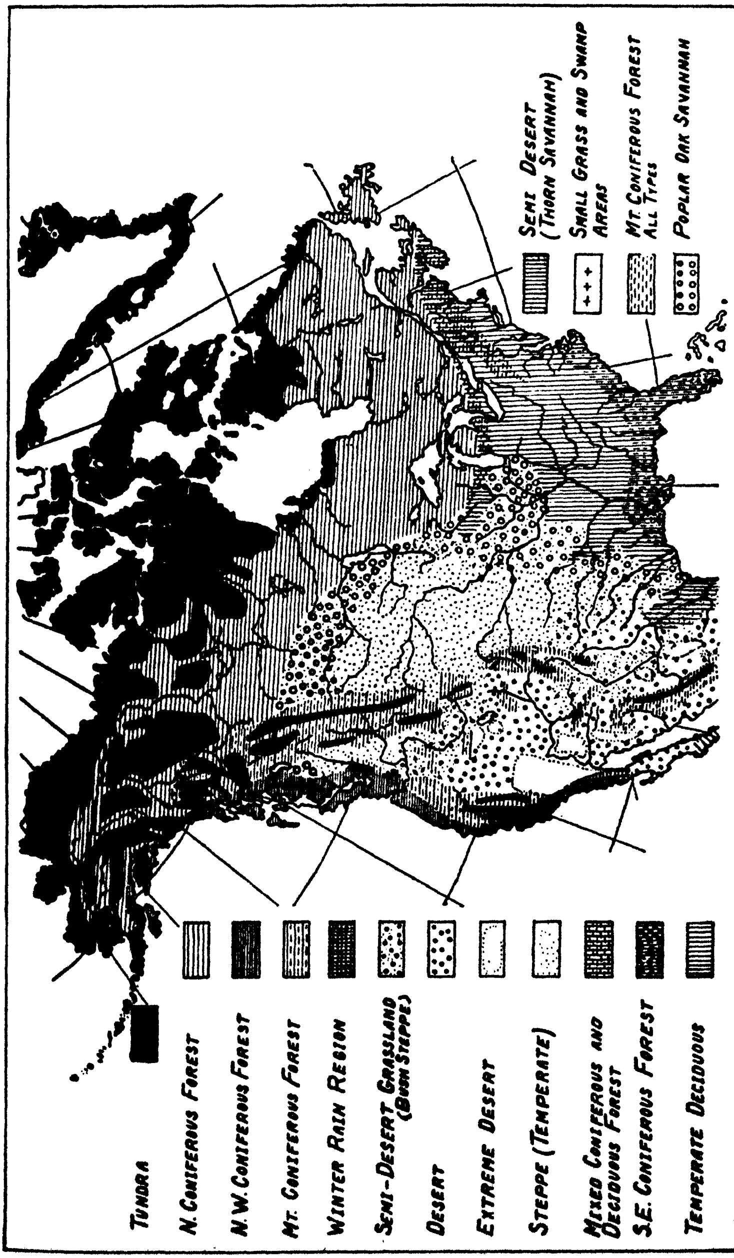


FIG. 32.—Biotic areas of North America. (*From Shelford, Jones, & Dice 1926.*)

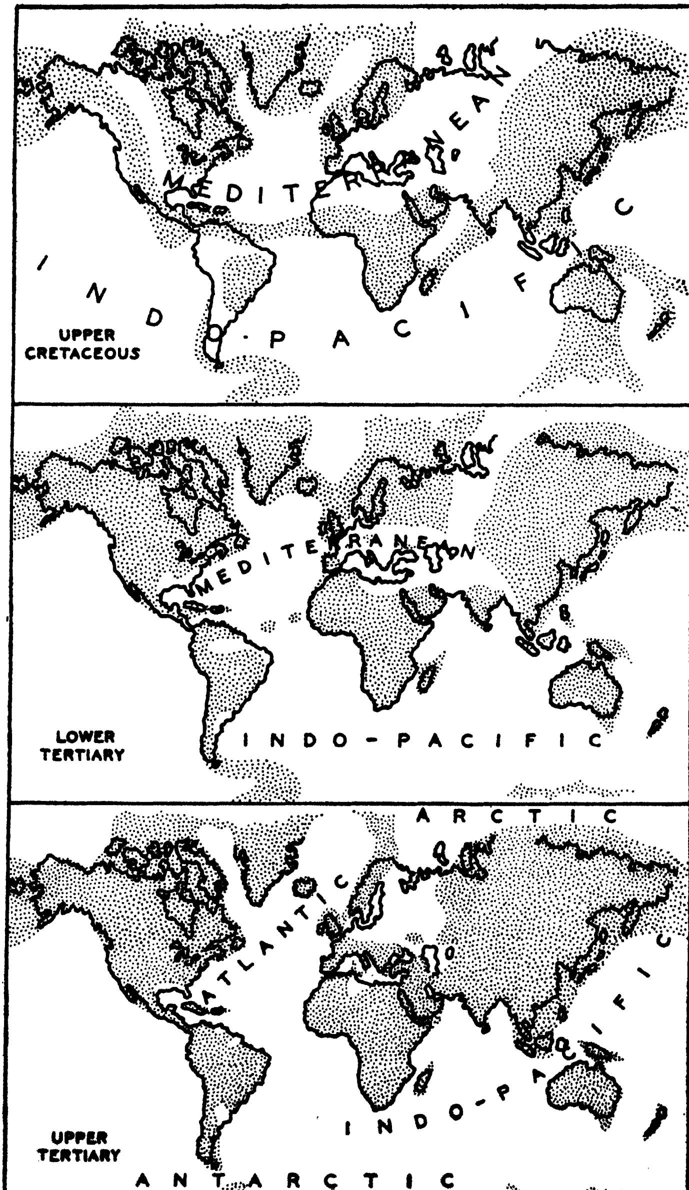


FIG. 33.—Distribution of water and land during Upper Cretaceous, Lower Tertiary, and Upper Tertiary periods. Dotted areas indicate the extent of land masses. (*After Ortmann* 1902.)

on small areas. This appears to apply to some groups but does not agree with the distribution of others. For example, dragonflies have excellent powers of flight and may cover an area more rapidly than a slowly emigrating plant (Calvert 1923, Bartenev 1930, 1932). In land habitats temperature is often the most potent factor in limiting the ranges of animals, and water perhaps ranks second; but many other factors may be important under various conditions. Water habitats are more or less stable in regard to temperature; salts, gases, and other solutes are often limiting factors in them. Sometimes closely related species have almost identical ranges; sometimes they occupy different areas which have different environmental characteristics. In general, wide-ranging species are spread over an area of monotonous environment, or they are able to live in a variety of habitats. Species of limited range are often confined to particular or local habitats.

Centers of Origin.—Animals as species are believed to have originated in particular regions on the earth and to have spread through contiguous areas as far as environment permitted. Each species thus has a center of origin. Adams (1909) has established criteria and formulated definite rules for determining centers of origin. Often it is difficult or impossible to discover such centers because ecological conditions have changed and optimum conditions for a species may have a different location from that which it had when it originated. In other cases it is possible to fix centers with some assurance. Ruthven (1908) found that American garter snakes originated in northern Mexico and spread over adjacent areas, with orthogenetic variation toward dwarfing, so that the species at the borders of the range are now small. Regions where environmental conditions make it easy for a species to spread constitute highways; and areas where some environmental factor or factors vary beyond the limits of toleration for a species are barriers. Animals may invade new regions by active emigrations; be carried on ships, railway trains, airplanes, and migrating animals; be transported on floating objects, swept along by winds or currents; pass along mountain ranges, over plains, or through shallow waters; etc. Barriers may result from conditions associated with mountains, valleys, wide expanses of water or desert, salt, prevailing winds, etc. New geographic races, which may be incipient species, originate at a point remote

from their main ancestral group; for their perpetuation they must expand rapidly or have a high reproductive capacity or both; races usually blend along the borders of the areas that they occupy (Meise 1928, 1936); races remain distinct only if there is centrifugal movement from the centers of both; barriers often account for the distinctness of subspecies, or races; no race is the result of a single mutation but an accumulation of several or many; a graded condition in a characteristic of an animal may be associated with a gradation in environment; a subspecies may result from natural selection or accumulation of environmental effects or both; a race may be adapted to a particular area but range far beyond it if there are no barriers; a subspecies which ranges over a diversified area may be a blend of several races—such are the conclusions of Sumner (1932) after years of study on the races of mice of the genus Peromyscus. Geographic races appear to become genetically stable, probably through the effects of genotypic variations and selection (Sumner 1932, Lukin 1935, Woltereck 1933). There are many cases known where races, species, genera, and larger groups have spread from centers and changed into new types as they invaded new areas. Often such emigrations can be correlated with environmental conditions. The population of land areas by animals was made possible by the development of a flora of high nutritive value (Campbell 1930). Angiosperms made possible highly organized animals of high metabolic rate (birds and mammals) (Werner 1936). Many times ungulates spread from centers in the Holarctic Region into continents to the south and evolved into types which are now peculiar to South America, Africa, India, and Malaya (Matthew 1915). Civilization has often changed environment. It has thus exterminated some species and permitted others to spread. Crop pests in Illinois under primeval conditions lived largely on restricted patches of prairie; but when land was cleared and devoted to agriculture, they occupied the new areas made available (Shelford 1915). Fraipont (1932) and his colleagues believe that distribution of faunas is to be explained by centripetal concentration of primitive forms which occupied a larger area rather than by emigration from centers; that centripetal movements are generally associated with specialization and senility; and that though mutations may give rise to varieties, they never cause new species, which are maintained to be brought

about by adaptation under the slow influence of environment and fixed by hormonic effects on genes.

SUCCESSION

Of all truths relating to phenomena, the most valuable to us are those which relate to their order of succession. On a knowledge of these is founded every reasonable anticipation of future facts, and whatever power we possess of influencing those facts to our advantage (Mill 1848).

Types of Succession.—Many changes on the earth take place in an orderly manner. Some are rhythmical, and systems involved attain temporary stability now in one place or time and now in another. Other changes are progressive and lead to comparatively steady environmental states. During geological succession there has been a gradually changing series of plants and animals associated with prevalent conditions on the surface of the earth. Some types have flourished for a time and then been exterminated; others have transformed their system of activities into new species which continued under new conditions of existence. At each period when the earth has remained fairly stable for a time, characteristic groups (communities, biomes) of plants and animals have successfully occupied and often dominated available habitats. Such successions always take place in an orderly, sequential manner. They are called "ecological succession."

Ecological Succession.—Ecological succession is a progressive and orderly series of changes to a climax (or biome, or formation) —in other words, to a more or less complex group of plants and animals which may continue to flourish and dominate an area in an essentially stable state because it fits existing climatic conditions. This succession is always progressive and toward a climax (Phillips 1934, 1935, 1935*a*), unless some disturbing factor, such as fire or overgrazing in terrestrial habitats or poisonous factory wastes in aquatic habitats, changes its course. When a great change opens up a new habitat for occupation, the area is first invaded by pioneers from surrounding areas. Often animals arrive before plants because they move more rapidly, but a pioneer community of plants and animals is soon established, and this begins to progress through few or many transitional stages to a climax. Pioneers on an area are often few in species but may

be numerous as individuals. Their struggle to survive in the new area is, as a rule, largely with the physical and chemical features of environment. But soon plants form a rather stable matrix; the animal members of the biome interpenetrate that and depend on it. During transition periods there are often varied conditions and a considerable number of species. As the climax is attained there often are again fewer species and more uniform conditions. "Succession comprises changes in community, change in species and in life forms, biotic reactions, and development of habitat

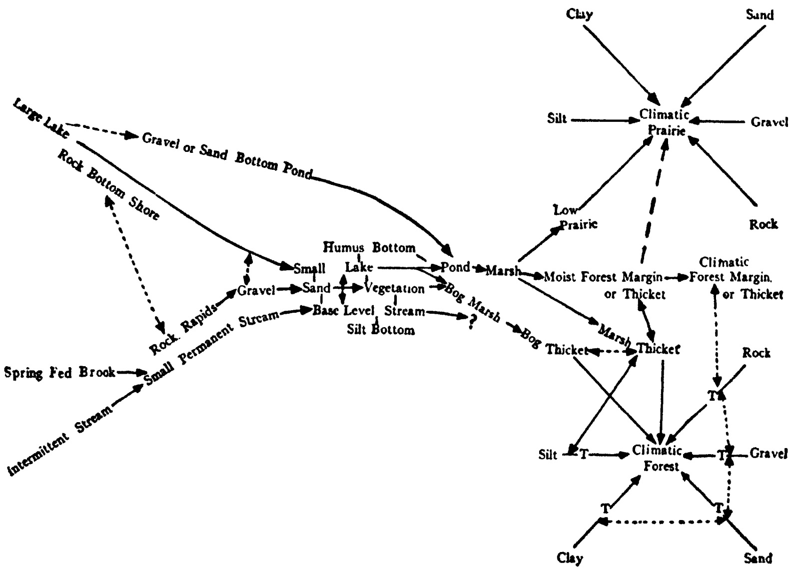


Fig. 34.—Succession in habitats as shown by Shelford (1912*b*) for the forest border region in central North America. The names indicate animal communities; *T*, thicket.

from an extreme to a medium or normal condition" (Phillips 1934). The rate and character of ecological succession may depend on topography or other factors, but in any particular region it is influenced primarily by climate. It is initiated by certain causes and continued by others. However, successions cannot be classified on the basis of causes but must be judged by their development. Succession is not merely change but a "sequence of phases" (Tansley 1935). When a bare rock face is exposed by a landslide, it is first invaded by mosses and lichens; such animals as ants, other insects, spiders, and snails may hunt over

it, but animals do not become established until a little soil and at least such covering plants as mosses are present; so the area progresses through a longer or shorter series of quite characteristic stages until a climax forest with its characteristic biome is the result. Stages in successions, especially on land areas, are commonly named for dominant plants because they are fixed and readily observed, whereas the animal constituents of a biome are often harder to discover and treat statistically.

Succession on Coral Reefs.—The growth of coral reefs brings about a peculiar type of ecological succession. The accumulations that give rise to inclosed lagoons are due primarily to the presence and activities of living organisms. Darwin and Dana were early advocates of the subsidence theory of reef formation by the upgrowth of fringing reefs while a coast was sinking. Semper advanced the view that fringing reefs might be formed by the dissolving away of the interiors of massive formations, thus leaving lagoons or channels surrounded by fringing reefs. Recent evidence has largely given support to the subsidence theory and also brought in glaciation as an important factor. During glacial times much water was lost from the ocean, and this furnished material for the glaciers. On this account the surface level of the ocean was lowered, and platforms were worn at the edges of exposed land areas. As the ocean gradually rose, reefs were built up on many of the submerged platforms (Vaughan 1919). Pioneer corals and other animals that become established on exposed reefs differ markedly in form of growth and other qualities from those that live in sheltered lagoons, the former usually growing as flat encrustations and the latter forming treelike growths.

Succession in Streams.—As streams usually move very rapidly when small and are turbid when large, they do not support much attached vegetation and therefore furnish an excellent opportunity to study succession in animals. Shelford (1911) did an excellent piece of work on succession of fishes in the streams along Lake Michigan. He found that pioneer species in small streams were also found at the headwaters of larger streams. In all streams the species of fishes were arranged in orderly sequence from source to mouth. As a stream grows older and longer its pioneer fishes remain near its source, and new species occupy the lower reaches of rivers as they develop. Fishes that enter a

stream or are displaced by floods will seek the level to which they are best adapted.

Succession in Ponds.—In a series of ponds of different ages which had been left along the shore of Lake Michigan, Shelford (1911*a*, 1911*b*) made another study of succession of pond fishes

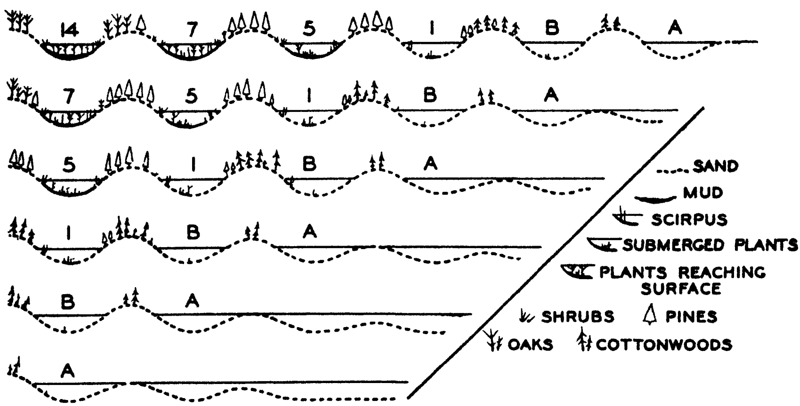
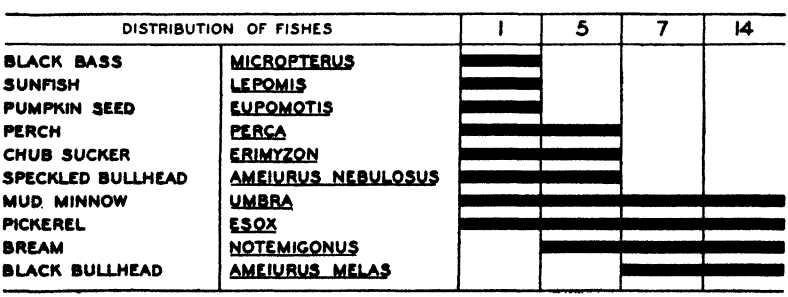


Fig. 35.—Succession as shown by a series of ponds and ridges, left as the level of Lake Michigan gradually fell. (*After Shelford* 1911*a*.) The upper horizontal series shows four representative ponds, the oldest (14) at the left, and two earlier hypothetical stages (*A*, *B*) at the right. The vertical series at the left shows the same series of stages as a pond gradually grew older on one locality, the oldest stage being at the top. The occurrence of characteristic fishes in the ponds may be indicated as follows:



(Fig. 35). Pioneer species of plants and animals were entirely replaced by other species. As ponds grew older, vegetation, total food resources, and bottom deposits increased. Then conditions for breeding became less favorable for pioneer fishes, which were dependent on clean bottoms. So ponds began with bass, sunfishes, and perch but just before becoming swamps

supported mud minnows and black bullheads. Some fishes flourished on clean, sandy bottoms; others found optimum conditions when there were some aquatic plants and bottom sediments; and others flourished when the water was choked with floating and emergent vegetation.

Climax.—A climax is the final stage in a series of successions. Clements (1916, 1935, 1936) has called a climax a "complex organism" which consists of plants and animals. It is confined to a restricted area, which may be continental in extent or very limited. Like an organism, it must fit its environment; and a climax is adapted to climate. A climax has ontogeny and phylogeny. It remains in "dynamic equilibrium." In North America the principal climaxes are tundra, boreal forest, deciduous forest, scrub, and prairie (Weaver & Clements 1938). In any particular region all successions tend to end in a monoclimax (Phillips 1935) or a polyclimax which may be climatic, edaphic, or physiographic (Tansley 1935). Some ecologists hold the view that succession can be brought about only by interactions of organisms (Phillips 1935); others recognize autogenic succession, brought about by organisms, and allogenic succession, which is due to external factors (Tansley 1935). There may be more or less of a mosaic of types; on account of variations in soil and other factors, succession may be accelerated or retarded, but the trend is toward one general type of biome. In a climax there is a limited number of dominant species. As long as environment remains constant these do not permit subdominant species to attain controlling positions. But dominants may vary with seasons and in different years. The biome is a harmonious, integrated whole but is not inflexible. It possesses ability to adjust itself to varying conditions.

Classification of Climaxes.—There have been various ideas as to the use of terms for ecological units among botanists and zoologists. Clements (1936) proposes to treat climax as a synonym of formation and, when both plants and animals are included, also of biome. Both he and Phillips (1935) believe that community should be perhaps used as a term that refers to groups of plants and animals without particular significance as to size or position in schemes of ecological classification. Clements (1936) and Shelford (1932) suggest the use of the following terms:

Climax (Formation)—a clearly defined group of dominants.
Association—largest subdivision of a biome; the "community" of plant sociologists has one or more dominants peculiar to it.
Consociation—usually characterized by a single dominant.
Fasciation—characterized by arrangement of dominants.
Lociation—fixed by local differences in grouping of dominants.
Society—groupings of subdominants.
Sociation—seasonal variations in societies.
Lamination—a layer society, as the strata in a forest.
Clan—a small, distinctive community of subordinate importance.

This scheme appears to be applicable to land biomes but meets difficulties in ocean and freshwater. It will be followed as far as possible by the writer, as it is one of the most carefully considered plans offered up to the present time. The difficulty has been that plant ecologists, foresters, animal ecologists, oceanographers, limnologists, parasitologists, pathologists, sociologists, and paleontologists are specialists. Each is interested in his own field and does not appreciate the points of view of those in other fields.

CHAPTER VI

RHYTHMS

Rhythms in Nature.—Natural phenomena are commonly rhythmic. "The formation of overtones from Nature's rhythms seems the only hypothesis capable of explaining the chief methods of Nature" (Reynolds 1920). In order to utilize energy and store products of work done, rhythms in which there are changes from stability to instability and back to stability are almost universal. Organisms appear to work most efficiently in rhythms. Reynolds recognizes steps in assortment as colloidal, enzymatic, biotic, and psychic. There are two types of biologic rhythms: (1) those correlated with periodic changes in environment, as day and night, tides, seasons; and (2) rhythms inherent in organisms and more or less independent of environment, as age cycles (Flattely 1920). Differences in rhythmic adaptations and adjustments are concerned with daily, lunar, annual, and sunspot cycles; alpine, frigid, temperate, and tropical faunas; periods of dormancy and activity; and periodic migrations.

Metabolic Rhythms.—There is no question that rhythms play an important role in vital phenomena and that animal activities are readily correlated with rhythmical environmental conditions. Fatigue results from the accumulation of substances that retard metabolic rate, and recovery is associated with their removal. When a gland cell is being loaded, its metabolic rate grows slower, and accelerates during discharge. During day a green plant carries on photosynthesis, manufactures starch, and its metabolic rate slows; at night starches are converted into sugars, transported away from synthetic centers, and metabolic rate increases. Periods of rest and activity or of definitely varying activities are correlated with the ebb and flow of tides, the periodic succession of day and night, lunar succession, the cycle of the seasons, and perhaps with rhythms having longer periods. The same species may vary in its rhythms in different localities in order to conform with environmental conditions.

The majority of the human race sleep each night and eat during the day, but the polar Eskimos, who live where nights are six months long, have very irregular periods of activity, eating, and sleeping. Some mammals breed only once a year at a particular, favorable season; others, in which breeding is not closely dependent on environmental conditions, breed at any time. A red-legged locust lays its eggs in the autumn; a flour beetle lays eggs at any season. Willey (1920) has described a nice dovetailing of periods of rest and activity in Ceylon. Certain palms served as roosts for crows at night and for fruit-eating bats by day.

Reproductive Rhythms.—The rhythmic activities of animals that are not closely correlated with environment are, as Flattely (1920) says, commonly associated with attainment of a certain age or stage in a life cycle. It has commonly been assumed that the process of aging in an animal's life cycle is irreversible and always progresses from youth to old age. Child (1916) denies this and gives instances where old cells grow young. He says, "life . . . is a cycle consisting of alternating periods of senescence and rejuvenescence." An animal's metabolic rate and growth rate usually gradually decrease throughout its life, probably because there is a progressive accumulation of inert substances. However, cutting a planarian into pieces or starving it makes it young; *i.e.*, its metabolic rate increases and proceeds at a more rapid rate. When a planarian is fed amounts above its basal metabolic needs, its metabolic rate gradually grows slower, and it becomes senescent. Some such activities, like the resorption of tadpoles' tails (Swingle 1922*a*), the development of broodiness in fowls (Pearl 1914), and menstruation, are associated with endocrine secretions. Hisaw (1924) discovered that female gophers cannot bear young without resorbing the pelvis in the region of the pubic symphysis, and such resorption normally takes place through the action of ovarian secretions when females have attained the proper age. By injecting ovarian extracts, Hisaw was able to bring about the resorption of the pubes in castrated males. When secretions that normally induce qualities that develop at certain stages in life cycles are absent, animals fail to make the usual progress. Castrated animals retain juvenile characteristics and do not develop adult characteristics. A eunuch has separate epiphyses on his long bones and does not develop a beard or a deep voice. During the

past decade there has accumulated an increasing body of evidence that shows that reproductive cycles are markedly influenced by light. Length of day may exert a profound influence on gonadal secretions and may induce migrations and other activities in animals.

DAILY RHYTHMS

Types of Daily Rhythms.—Most animals show more or less adaptation to the daily rhythmical changes that are brought about by the rotation of the earth on its axis. Animals may be arranged in three groups, according to responses to such cyclical changes: (1) those with periods of rest and activity which are correlated with daily environmental changes and vary as environment does; (2) those which have established physiological rhythms in their bodies which usually correspond to daily environmental cycles but which continue whether environment passes through its usual periodic variations or not; and (3) those which show a rhythmical behavior, without particular reference to daily environmental cycles. Welsh (1938) has reviewed these.

Periods of Daily Activity.—Linnaeus devised a floral clock, so that he was able to tell the time of day by a glance out of his window to see which flowers were open. The same may be done by observing the activities of certain animals. Birds begin and end their daily song (Seppa 1938, Palmgren 1932, Shaver & Walker 1931) and leave and return to their roosting places (Nice 1935) at particular times. Fireflies of various species begin to flash at different times after the sun sets (Buck 1937, Rau 1932). Some animals are active all day long; others, for only short periods. Oysters may regularly feed as long as 20 hours per day (Nelson 1921, Hopkins 1931). They are least active in early morning and most active in late afternoon. Some species of bats fly about all night; others are active only just after sunset and before dawn (Moffatt 1905, Welch & Griffin 1936). A barnacle high up on a rocky beach may be able to average 1 hour of feeding out of 24. The little pulmonate snail (Onchidium) which lives on Bermuda beaches devours algae only about an hour and spends the remainder of each day resting in its home crevice (Arey & Crozier 1921). It always feeds when the tide is out and during daylight.

Factors That Influence Daily Rhythms.—In the daily cycle of variations that influence the behavior of animals, light, humidity, and temperature are usually most potent as stimulators of activity or quiet. Terrestrial insects are greatly influenced by these three factors. Many of them resort to special localities and assume sleeping positions at night (Rau 1916). Certain wasps build a cell every day and seal themselves inside each night. Next morning the cell is stored full of provisions, and an egg is deposited in it; then another cell is built. Many animals appear to be influenced by the absolute amount of light, and their times of activity vary on cloudy and sunny days. Other animals (slugs, etc.) are not so responsive to changes in light but are more influenced by variations in humidity and temperature. Terrestrial insects are usually more active during humid periods than in dry weather, but rain causes them to become quiet (Carpenter 1934, Eckstein 1934, Park 1931).

Nocturnal, Crepuscular, and Diurnal Animals.—Species of animals tend to segregate so as to avoid competition and enemies. Such segregation pertains not only to space but also to time. During light and dark there are processions of active animals, each adapted to some food, temperature, humidity, or light intensity that obtains at some particular period of day or night. Some animals become active as soon as the sun sets, others 2 hours later, others at midnight, and others at 2 A.M. Various species of mosquitoes suck blood at particular hours during night; others feed only by day (Shannon 1934). Mutillids burrow underground each night and thus escape unfavorable temperature and humidity changes (Rau 1922). In deserts, glistening sandy surfaces are superheated during day and, as lack of moisture permits rapid radiation, very cold at night. Small, poikilothermic desert animals are commonly crepuscular and thus escape extremes. Butterflies are usually diurnal, and moths are nocturnal. Each is adapted to its group of environmental conditions. White, night-blooming flowers are commonly pollinated by moths; gaudy day-blooming flowers, by such diurnal insects as butterflies, flies, and bees.

Daily Plankton Migrations.—Light and changed responses to gravity have long been recognized as potent factors in the daily migrations of plankton animals from deep to shallow waters at night (Loeb 1893). But, though it is generally known that most

plankters respond to light, the case is not a simple and direct response to light intensity (Juday 1904). Many plankton animals avoid strong light but are positively phototropic to low intensities; some species do not migrate, all individuals of responsive species do not migrate every day, some migrants merely move to and from lower and higher levels at some distance beneath the surface, some species remain in the epilimnion and others move from the hypolimnion to the surface, some arrive at the surface soon after sunset and others just before sunrise, etc. In the Gulf of Maine, Clarke (1933*a*, 1934) studied the behavior of three species of copepods. One inhabited the eplimnion (p. 276), another was irregularly distributed, and a third was found in the hypolimnion during day. Most individuals of the first species (*Metridia lucens*) went to the surface at night, apparently because the females responded to light and the males followed them (Parker 1902). In all three species larger, and older, individuals lived at lower levels than smaller. In Japanese lakes Kikuchi (1930, 1933) has found segregations in species and differences in behavior similar to those described by Clarke in the ocean.

Inherent Physiological Rhythms.—Animals living in a variable environment to which they are adapted always have some powers of adjustment to fluctuating variations. When such variations are rhythmical, adjustments frequently become incorporated into the physiological constitution of an animal and continue even if the environment ceases to fluctuate in the usual way. The little shrimp, *Hippolyte varians*, which lives on seaweed along the coast of Great Britain, matches with great fidelity the color and pattern of the background on which it rests during the day but turns green at night. If kept continuously in light or dark, the shrimp continues its rhythmical color changes at approximately 12-hour intervals for several days (Keeble & Gamble 1904). The white grub of a scarabaeid beetle, *Cotinis nitida*, commonly emerges from its burrow and creeps out of the surface of the ground at night, when it is least subject to attack by predaceous enemies. When kept continuously in light or darkness at constant temperature the grub continued to come out rhythmically for several nights (Hintze 1925). In his studies of forest animals Park (1935) found that a wood-boring beetle (Passalus) showed no daily periodicity but that a litter-dwelling millipede (Spiro-

bolus) did to a striking degree. Bats show rhythmic, daily periods of activity for two weeks or more when kept in unvarying environments (Welsh & Griffin 1936). Pigeons, whether feeding or fasting, show daily variations in metabolism, with a decrease at night. These are independent of food, sex, or age. Owls show similar periodicities, but the lowest level is during day (Scharnke 1932). A remarkable case of daily variation in reproductive activity is in the filarial worm, *Wuchereria bancrofti*, which is inoculated into man by a mosquito. It produces swarms of living larvae in the blood of its human host at night and hence was called by older parasitologists *Filaria sanguinis nocturna.* If its host sleeps at night and works during the day, the larvae appear in the blood by day. Another filarial worm is transmitted by a diurnal tabanid fly and produces larvae in man's blood by day. A third filaria which is transmitted by a sand fly which bites both day and night has larvae that live in dermal lymph spaces and shows no periodicity. The length of the asexual cycles of certain sporozoan parasites in birds may be made longer or shorter by subjecting the hosts to days and nights of varying lengths (Boyd 1929; Boughton, Atchley & Eskridge 1935). The physiological state of the host thus modifies the rhythmical reproductive cycle of the parasite.

LUNAR RHYTHMS

Effect of Moon on Tides.—The movement of the moon on its orbit around the earth produces two rhythms which are of considerable importance to animals: (1) the tides ebb and flow twice each day; and (2) the height of tides varies rhythmically, spring tides occurring every two weeks when the pull of the sun and that of the moon reinforce each other, and neap tides when the gravitational forces from these two bodies act at right angles. Not only does the height of water vary with changes in tidal cycles, but littoral marine animals are also subjected to fluctuations in force of currents, temperatures, salinities, etc.

Lunar Rhythms in Sea.—In littoral marine biomes there are many instances of lunar cycles of activity. Certain algae (Dictyotaceae) have been recorded by various observers as freeing their gametes at certain phases of the moon. Among animals probably the most famous lunar rhythms have been demonstrated among the palolo worms. The Pacific palolo,

along the shores of Fiji and Samoa, comes to the surface in great swarms to spawn when the moon is full in October and November. The Atlantic palolo (Mayer 1902) swarms within 3 days of the time of the moon's last quarter between June 29 and July 28. The hinder portion of the worm crawls out of the burrow and breaks loose from the anterior. It darts to the surface, rapidly swims backward while shedding its eggs or sperms, and the whole ocean becomes milky. Other polychaete worms besides the palolo show a correlation between their spawning and the phases of the moon (Ranzi 1931, Guberlet 1934). Grave (1922) says:

> The cause of this type of periodicity must be fundamentally the same in all cases, although it is exhibited in a variety of ways and at different times relative to the phases of the moon.

In speaking of *Amphitrite ornata*, Scott (1909) says:

> The egg-laying reflex is closely associated with the time of spring tide; the height of any period of egg-laying always occurs within two days of the time of new or full moon. Periods of oviposition occur in June, July, and August. The moon does not have any direct influence in producing the period of sexual activity. It is probable that the tide also has little, if any, direct effect on the process. At any spring tide, the worms feed more actively, the food supply is more abundant and the sand flats have a higher temperature. As this period approaches we also find a more rapid growth and development of immature eggs and sperm. Therefore the period of sexual activity is closely associated with a synchronous period of greater bodily activity, and this greater vigor of the animal is induced by conditions that depend upon the tide. In this way we may explain how oviposition in Amphitrite has become a sort of reflex habit associated with the time of spring tide.

The Atlantic palolo gives off more carbon dioxide as the time for spawning approaches (Treadwell, 1915). Spawning periods at various phases of the moon have been described in corals (Marshall & Stevenson 1933), chitons (Grave 1922), clams (Battle 1932), and other marine animals. Catches of herring are also said to vary with lunar phases (Savage & Hodgson 1934).

The Grunion.—Thompson (1919) has described the very interesting behavior of a smelt, the grunion, *Leuresthes tenuis*, along the California coast. The little fishes of this species come on the second, third, and fourth nights *after* the spring tides during April (March, May). They come exactly at high tide

and wiggle out on sandy beaches above the water. The females bury their posterior ends in the sand and the eggs are deposited 2 to 6 in. below the surface, each female producing about 2,200. Each is attended by a male which exercises his fertilizing functions. The eggs are protected from enemies and are able to stand rains or considerable desiccation. After two weeks the eggs are ready to hatch but will not do so unless the egg pod is washed out of the sand by the tides occurring at the next dark moon. The fry within the eggs will live for a month if they are not exposed by the spring tides.

The grunion offers a remarkable instance of adaptation to lunar rhythms as represented by tidal fluctuations. If spawning occurred just before the highest tides, when the high beach was being eroded, instead of just after, when the beach was being built up, the eggs would be washed out of the sand before they had developed for a fortnight. If spawning occurred at the very highest tides (dark of the moon), the eggs might not be exposed for a month or even for two months. If grunions laid their eggs during the day, they would be exposed to the attacks of gulls and other predaceous animals. A female grunion may deposit a pod of eggs every 15 days during May, June, and July on certain parts of the California coast (Clark 1925).

Lunar Rhythms in Freshwater and on Land.—The influence of lunar cycles on animals outside littoral marine biomes is meager and usually unsatisfactory. A correlation has been demonstrated between the amount of plankton in certain rivers and phases of the moon (Thomson 1911). Similar correlations have been reported for the spawning of the ectoparasites of freshwater mussels (Ray & Chappraverty 1934). Ramanathon (1932) recorded the times of 2,457 matings of the Indian buffalo and constructed distribution curves. Cows came in heat most often on the day of the new moon and frequently on the day of full moon. There are many superstitions concerning the planting of crops and other matters in relation to phases of the moon, but they appear to have no scientific basis.

ANNUAL RHYTHMS

Earth in Relation to Seasons.—The annual revolution of the earth about the sun and the inclination of the earth's axis to the plane of the ecliptic produce a regularly recurring series of sea-

sonal changes which are most pronounced near the poles and least near the equator (Fig. 1).

Adaptations of Animals to Seasonal Changes.—The activities of many animals are closely correlated with the annual succession of seasons. In temperate and frigid regions hibernation is common during periods of cold; in the tropics animals often aestivate during dry or hot periods. The annual cycle of many species of animals is made up of a series of stages in a characteristic life history or of a characteristic series of periods of rest and activity which are closely correlated with seasonal progression. The development of different species begins at different times in the general climatic cycle, and there is thus a progression throughout the year. The time of activity of each species must conform more or less with environmental opportunities for feeding, the presence of optimum temperatures, proper conditions for reproduction, etc. Particular species may vary markedly in numbers at different seasons. This is strikingly shown by plankton organisms. As the season advances, each species reaches a maximum, then declines, and may be succeeded by another species. Long-established correlations operate in such a way that seasonal environmental changes serve to stimulate animals to appropriate activities or inactivities, and cyclical physiological changes within animals prepare them to react properly with recurring seasonal events. The rate of metabolism of poikilotherms varies more or less directly with temperature, but the relative rate in fishes is greater in cold than in warm water, and they therefore remain active there (Wells 1935). The number of red blood corpuscles in a typical lizard increases as the animal's blood thickens in becoming adjusted to cold resistance (Weigmann 1931). The kidneys of frogs undergo marked seasonal changes in structure (Tsui 1931). In winter, resting glomeruli are contracted and empty, there is no mitosis; in spring, glomeruli expand, tubule cells have papillae containing hyaline secretions, and mitosis is common; in summer, glomeruli are turgid, tubules contain alveolar secretions, and mitosis occurs in most cells; in autumn, conditions are similar to those in spring. A frog's heart beats more rapidly in summer than in winter, perhaps because the thyroid gland secretes more actively (Carter 1933). Even the body temperatures of birds are lower in winter than in summer (Simpson 1912).

Seasonal Variations in Animals.—Herdman (1909) has classified as follows the factors that influence the numbers of plankton organisms: (1) sequences of stages in normal life histories, (2) irregularities introduced by interactions of different organisms, and (3) more or less periodic abnormalities, as to time and abundance, caused by physical changes in weather. Johnstone (1908) gives diagrams that show the seasonal appearance of the eggs of certain marine fishes and of various plankters off the west coast of England. Diatoms, which are the chief source of organic food for animals, decrease in May but increase again in November and remain abundant through the colder months. There is the greatest quantity of plankton in winter, but the greatest variety in summer. The chemical characteristics of the water in Lake Mendota vary considerably with seasonal successions (Birge and Juday 1911). Such variations are brought about chiefly by fluctuations in temperatures and gases, but the activities of living organisms also exert a considerable influence. Similar changes have been observed in a reservoir in Calcutta (Pruthi 1932). The yellow perch in Lake Mendota accumulate stores of fat within their bodies during the summer, and these are used up in winter (Pearse 1924). Juday (1922) made quantitative catches of the fauna in the deeper waters of Lake Mendota and found that some of the animals showed striking variations in numbers at different seasons. The larvae of the midge, *Chaoborus punctipennis* Say, varied from about 1,000 per square meter in August to as high as 25,000 to 30,000 in December. Birge (1897) studied the variation of plankton animals in Lake Mendota and described the seasonal maxima for various species. The chief factors causing seasonal variations were said to be (1) quantity and quality of food, (2) temperature, and (3) competition. In 1895 Cyclops varied from about 25,000 per square meter of lake in January to about 1,000,000 at the end of May. In his studies of the prevalence of acanthocephalans, Van Cleave (1916) observed that some species occurred in their appropriate hosts throughout the year and that others were found only at certain seasons. He states that important factors in determining the seasonal range of these parasites are (1) the longevity of their adult hosts, (2) time during which infection may occur, (3) time required for larvae to develop in intermediate hosts, (4) migrations or seasonal changes in food habits of hosts. The eggs of a parasitic worm (Nemato-

dirus) were counted in the feces of a llama for two years by Zawadowsky and Zvjaguintzev (1933). Ten times as many eggs were found in July, August, and September as in winter and spring. The worm lives for about six months in its host; and though eggs remain alive in winter, there is little chance for reinfestation then in Russia, where these observations were made.

Light and Annual Rhythms.—On account of the relation of light to photosynthesis, length of day is a dominant factor in the seasonal periodicities of most plants, though variations of temperature and water are also important. Most animals are directly or indirectly dependent on vegetation, and their development is often closely correlated with that of food plants. Length of day also affects animals directly in that diurnal or nocturnal species are active or inactive for longer or shorter periods of time. The duration of light stimulation certainly is effective in inducing particular physiological states in animals, even when they are kept at constant temperatures. Prolonged exposure to light causes the gonads of fishes (Hoover 1937), amphibians (Bissonnette 1935), reptiles (Clausen & Poris 1937), birds (Bissonnette 1935, Cole 1933, etc.), and mammals (Bissonnette 1935, etc.) to develop. Aphids show remarkable and characteristic responses to various time periods of illumination (Shull 1928). At certain temperatures in continuous light aphids are wingless; in continuous dark a few winged forms develop; in 8 hours light and 16 hours dark almost all are winged. These effects are not brought about through plant food but by direct effects of light on aphids themselves.

Temperature and Annual Rhythms.—Temperature, directly and indirectly, is an important factor in seasonal cycles. The maxima in numbers of certain species are closely associated with high or low temperatures. The rate of metabolism and behavior are often influenced by temperature. Perhaps no other factor so manifestly sets off such a variety of seasonal activities or states as does rising or falling temperature. In the ocean adjacent to northern Europe, seasons of low temperatures are associated with the penetration of light to greatest depths and consequently with maximum production of food in deep water. Many marine animals in that region spawn during the cold season (Ekman 1920). As has been stated elsewhere, Orton (1920) has pointed out that most marine animals fall into general

groups which spawn (1) when the temperature of the ocean falls or (2) when it rises. Cooke (1913), although admitting that the migration of such birds as the American robin is influenced largely by average temperatures, shows that "the temperature under which the birds[1] are migrating is about four times as variable as the date of arrival of the birds." He points out that it is rather difficult to judge of the effects of temperature on bird migration because the temperatures at which birds leave distant localities may be quite different from those at which they arrive at points of observation, and it is difficult to determine how far birds have traveled. A favorable temperature may stimulate a bird to start off, and the bird may then encounter unfavorable temperatures while migrating. In many localities in the tropics there is little annual variation in temperature and little variation in the seasonal rhythms of animals. In temperate regions a season of low temperatures may retard the growth of animals and prolong their life histories, thus causing those that are annuals to become biennials and producing other aberrant conditions. A mild winter may advance the times of breeding of animals during the following spring (Keyser 1934).

Annual Variations in Available Water.—Seasonal variations in the amount of available water are often concerned with successions. Morgan (1907) believes that the seasonal dimorphism of certain butterflies is due largely to varying conditions of humidity. Wolcott (1918) points out that prairie animals are apparently most abundant in spring, and he believes this to be due largely to the fact that moisture conditions then permit more isopods and earthworms to frequent the surface layers of the soil. Cummins (1920) observed that migration "waves" of frogs to aquatic habitats for spawning were coincident with periods of high relative humidity, when the temperature ranged from 16 to 26°C. Sanders and Shelford (1922) state that the animal population of the sand dunes near Chicago during summer, in general, varies directly with the evaporating power of the air and, therefore, with the amount of water available for animals. Cooling air has the effect of drying it, because it can hold less moisture at low temperatures. It then has less evaporating power, but, if suddenly warmed, it tends to dry out animals

[1] American robin, fox sparrow, towhee, brown thrasher, rose-breasted grosbeak, ovenbird, Baltimore oriole, scarlet tanager.

rapidly. So temperature variations influence availability and loss of water in terrestrial habitats.

Animals of Various Seasons.—The chief physical variants during annual cycles of seasonal changes are light, temperature, and available water. These, directly or through their influence on vegetation and available food, are the most important environmental factors that are concerned with seasonal cycles. In temperate regions of the earth there are characteristically "winter" and "summer" species. Certain apterous insects and amphipods reach their numerical maxima during cold weather; the fairy shrimps are present in the cool, temporary puddles formed by melting snow and early spring rains; frogs and toads are active only during the warmer months. Some animals, like the ptarmigan and varying hare, change their coats and are white in winter. Morgan (1907) maintains that cool climates tend to make butterflies lighter in color and that warm climates bring out richer and deeper shades. Many of the so-called winter and vernal animals of temperate zones have relatives that are found in arctic or alpine habitats, and those that are active in summer often show affinities with the animals of the tropics. Ekman (1920) believes that the relict faunas of Scandinavian lakes and fiords show their relationship to marine ancestors by breeding during the cold season, which, for the species concerned, is apparently the best time of the year for obtaining food and rearing offspring. In any particular locality and habitat certain animals will be active at the same season year after year. This is true of the plankters in the ocean (Fish 1925), the communities of animals along seashores (Johnson & Miller 1935), the societies in prairies (Isely 1937), and elsewhere.

> Species differ in time in annual climatic cycle in which development begins, in time of occurrence of dormancy and in the conditions necessary to break it up, in threshold of development relative to several climatic factors, in velocity of development relative to several climatic factors, food, etc., and in size and total energy expended (Shelford 1918).

A successful species must fit into the seasonal rhythm that prevails when and where it lives.

Reproduction and Annual Rhythms.—Among the varied activities of animals, those connected with reproduction per-

haps show the most striking adjustments to usual annual rhythms, but in this connection it should be said that the cyclic, physiological, successional phenomena related to reproduction often persist when the external environmental conditions that are usually associated with them are lacking. Schultz (1912) cites instances where plants and animals that were transferred from the Southern to the Northern Hemisphere bred at the same season as before their transfer. He points out that, though all animals do not breed at one season, many species do breed at a particular season and that the particular time, though it may be correlated with favorable conditions in relation to season or to a favorable environment in general, is in most cases fixed by cyclical physiological activities. These activities may continue to cause a periodic ripening of the gonads when usual environmental changes are absent, and this may be true even when environmental conditions are not well suited to reproduction. On the other hand, some species of animals readily change their season for breeding, particularly under conditions of domestication. The wild hog breeds in November, and domestic strains breed at any time of the year. Schultz shows that related species may be able to occupy the same territory and that each may exist in greater numbers because it breeds at a different season from its relative. Along the Amazon, *Caiman niger* breeds during October and November, and *Caiman sclerops* in May and June. Adams (1907) states that crayfishes fall into two groups in regard to time of breeding: (1) cold-water species, breeding more or less throughout the year; and (2) warm-water species, mating in the autumn and laying eggs in spring. Reproduction is apparently the chief driving force behind the annual migrations that many animals make to and from their breeding grounds. Among some species of animals certain types of reproduction are associated with particular seasons. Many cladocerans and aphids reproduce by parthenogenesis during the warmer months, when there is an abundance of food, but produce fertilized eggs, which are usually quite hardy, in the autumn.

Causes of Reproductive Cycles.—Papanicolaou (1923), in discussing the reproductive activities of certain animals, says:

Considering the phylogeny of mammals, we find that the earliest living types actually display the polyoestrous rhythm just as do the

somewhat more recent and modified types, such as the insectivores or the rodents, among which polyoestrus prevails especially in tropical climates. But in the still earlier or lower animal a type of sexual activity exists which we may call monoestrous or seasonable, since the reaction shows a definite connection with certain seasons of the year. Birds, reptiles, amphibians, fishes, insects, molluscs, worms, etc., all show the same periodical expression of their sexual activities. The connection between the monoestrous rhythm and certain seasons of the year is equally well expressed in the mammals. The spring and the fall, the two most favorable seasons of the year, are usually those during which most sexual activities are shown, while the two extreme seasons. summer and particularly winter, are characterized by a more or less pronounced sexual quiescence.

During the past few years there has been great interest in mechanisms that control sexual cycles in animals, and many papers have been published in that field of investigation. Marshall (1936) classifies factors that determine sexual periodicities as endocrine, nervous, and environmental. The mere sight of an incubating female will stimulate the secretion of crop milk in a male pigeon (Witschi 1935). A sparrow usually lays about half a dozen eggs, but if eggs are removed continually from its nest, so that only one is present, as many as 50 may be laid. Broodiness in fowls is apparently stopped by the release of a hormone, prolactin. If this is not secreted, a bird may continue to attempt to brood, whether eggs are present or not. The laying periods of domestic fowls may be prolonged by the use of artificial light. Many instances are known of the stimulation of gonad development by light. Intimate relations have been demonstrated between pituitaries, adrenals, and gonads in vertebrates. Among aphids Shull (1929) found that at low temperatures many gametic females were produced; and at high temperatures, mostly parthenogenetic females. Reproductive cycles depend upon the interaction of various factors: genetic, physiological, and environmental (Bissonnette 1936).

ANNUAL MIGRATIONS

Seasonal Migrations.—Many animals make more or less rhythmical migrations which are correlated with the changing conditions brought about by the annual procession of seasons. Wodsedalek (1912) speaks as follows of the Heptagenia nymphs in Lake Mendota:

> All summer these insects occupy a narrow strip, about 3 feet wide, along the lake shore . . . Along in the latter part of October as the water turns cool the nymphs slowly begin to migrate into deeper water and practically all desert the shallow water before the ice begins to form. A careful search was made on the day the ice broke up in the spring, but not a single specimen was seen. A few days after the ice disappears, however, the nymphs begin to make their appearance.

Phryganea larvae in a European lake were observed to ascend Potamogeton plants and make cases from them in summer but in January to retreat to the bottom and use the accumulated leaves there for building (Wesenberg-Lund 1911). In Douglas Lake, Michigan, seven species of pulmonate snails migrate into deep water when cold weather comes and return to shallow water in spring (Cheatum 1934). When in deep water their pulmonary cavities are filled with water. Along the shores of the ocean such animals as crabs, prawns, lobsters, and squids go into deep water in winter and return to the shore in spring. Two brackish-water snails, Ilyanassa and Littorina, migrate up streams during summer retreat to deeper and saltier water in winter (Batchelder 1915). Migratory marine and freshwater fishes fall mostly into one of two classes: (1) anadromous species migrate inshore and often ascend rivers to spawn; (2) catadromous species spawn in deep water at favorable seasons and move into shallow water or streams at other times. Meek (1916) divides marine fishes into three groups: (1) midocean spawners which produce pelagic or bathypelagic eggs and the young of which frequent open water (eel); (2) coastal or subcoastal spawners with pelagic eggs and denatant (swimming or drifting with currents) larvae; and (3) coastal or subcoastal spawners with demersal (on or near the bottom) eggs. Whales, walruses, seals, turtles, snakes, and other marine animals also make seasonal migrations. On land, there are various types of seasonal movements: birds and certain bats go north or south; monkeys, deer, and wolves move up or down mountain slopes; caribou move from woodland to tundra or vice versa; buffalo and antelope follow the green grass as spring moves north and retreat again when cold drives them south; land crabs go down to the ocean to deposit their progeny in the ancestral habitat of their race. Certain mammals, like the hare, woodchuck, bushy-tailed wood rat, and muskrat, are accustomed to wander far from their usual ranges and habitats

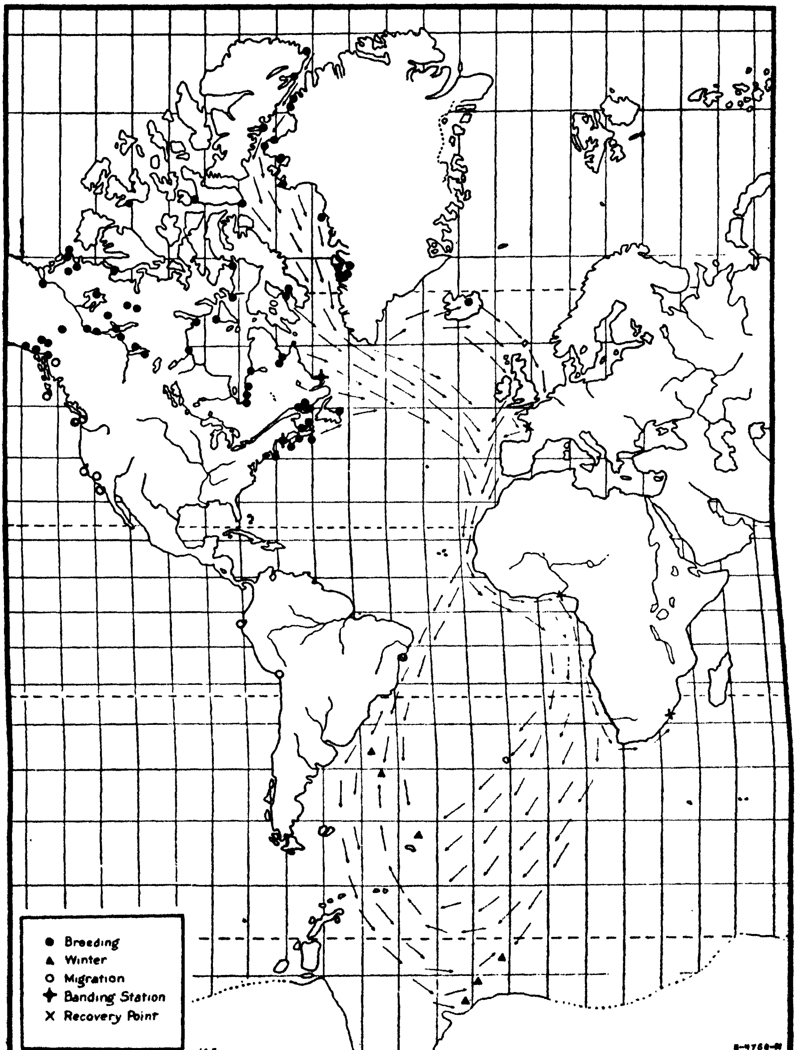


FIG. 36.—Distribution and migration of the arctic terns of eastern North America. No other species is known to breed in North America and cross the Atlantic Ocean. The extreme winter and summer homes are 11,000 miles apart. These terns fly about 25,000 miles each year. (*From Lincoln* 1935, *courtesy of United States Biological Survey.*)

at certain seasons (Anthony 1923). Bats, like birds, carry on extensive migrations and return to the same localities in succeeding years (Eisentraut 1936).

Reasons for Migrations.—Stubbs (1912) states that the present balance of life on earth is made possible by the existence of a mobile mass which is shifted twice yearly from hemisphere to hemisphere. Animals depend on plants for food; plants require sunlight, water, minerals, and carbon dioxide. So, when sunlight or necessary food materials fail, most animals must follow the sun, die down with the plants, or hibernate. During the northern winter the land and freshwater habitats have their productivity greatly decreased. Food, temperature, and breeding are the factors to which animals are able to make better adjustments by migrating. For example, a bird that goes to the arctic regions to breed in summer finds abundant food, long hours of daylight for foraging and attending to its young, and temperatures that, while often low, are not near its limit of toleration. When the arctic winter begins, many animals migrate south to escape the long night and the covering of snow and ice that makes food hard to obtain (Lincoln 1935).

Causes of Migrations.—Though migratory animals obtain certain advantages, it cannot be said that unfavorable variation in any one factor (such as a failure of food or a shortening of the hours of daylight) is the cause of all migrations. In his book on bird migration Coward (1912) says:

> Isepipteses and magnetic meridians, coast lines and river channels, food supply and sex impulses, hunger and love, homing instincts and inherited or acquired memory, thermometer, barometer, and hygrometer may all be factors in the problem; but none of them, and not all such together, can satisfy the whole equation.

Migration is not due to temperature alone. Swallows leave for the south when temperatures are high; herring gulls remain as far north as they find open water that contains fish or other food. Migration is in some cases due directly to lack of food, but in other cases animals leave abundance and invade regions where there is as yet little to sustain life. With a few exceptions, birds breed where they can find long days and an ample supply of food for their nestlings; salmon leave the ocean and, after fasting and traveling for weeks, lay their eggs and usually die.

There is an increasing body of evidence that animals, especially vertebrates, that make annual migrations show photoperiodism (Bissonnette 1931, 1932, Cooke 1935, Heape 1931, Hesse 1922, Lincoln 1935, Roberts 1932, Rowan 1926, 1931, Stimmelmayr 1932, Wetmore 1926). Increasing length of day stimulates endocrine glands (pituitary, etc.); secretions from them in turn

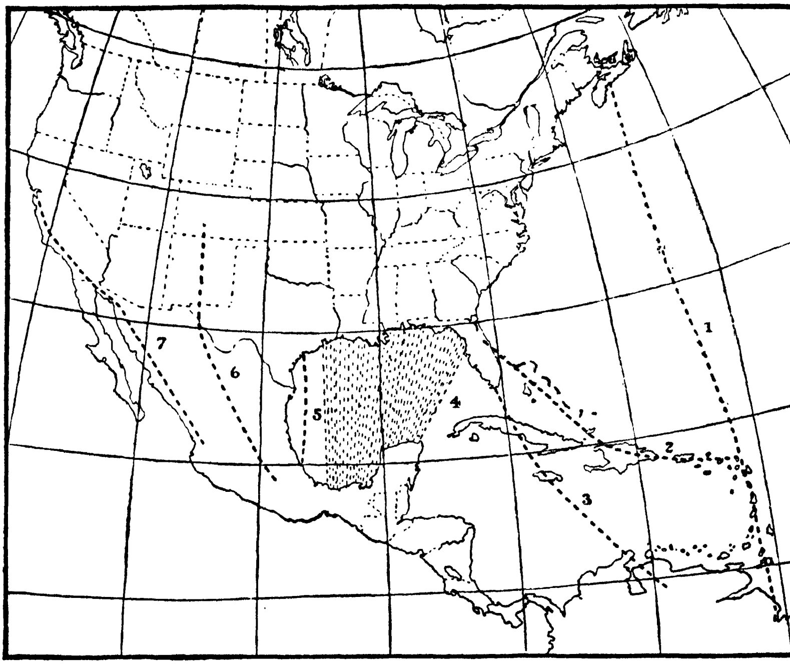


Fig. 37.—Principal migration routes used by birds in passing from North America to winter quarters in the West Indies and Central and South America. Route 4 is used most extensively; only a few species take Route 1. (*From Lincoln* 1935.)

stimulate gonads to development; and animals then migrate to breeding grounds. In Africa migrations by birds have apparently been influenced greatly by periodic failure of food supplies (Roberts 1932).

Origin and Evolution of Migrations.—There has been much discussion concerning the origin and evolution of the annual migrations of animals. In general, migrations are between breeding grounds and feeding areas, and the former are often more localized than the latter. Some individual animals return

to the same spot to breed year after year. There is evidence to show that, though particular flocks of birds from the same breeding area commonly migrate to particular feeding grounds at certain seasons, there is a tendency to make exploratory movements, and species often become established on new feeding grounds, which they then continue to visit each year (Leopold 1923). It is a noteworthy fact that most migratory birds move north in the spring and nest in the cooler parts of their ranges. Attempts have been made to explain this by the supposition that birds were forced to move south during glacial times and later followed the glaciers north as they retreated. Having thus established relations in the north and south, a semiannual migration was supposedly developed. Another theory emphasizes the fact that the continents in the Northern Hemisphere expand toward the north, whereas those in the south taper off toward the antarctic. With this in mind, it is plain that more nesting areas in land, marsh, and freshwater habitats will be available during the open season in the north. Some believe that the great feeding and breeding areas available in the north have attracted birds and led to the establishing of regular spring and autumn journeys. Walter (1908) gives a condensed but rather complete review of the numerous attempts to account for bird migrations. The well-established migrations of fishes may take place annually or only once when a certain stage in the life cycle has been reached. The adult yellow perch migrates into shallow water and spawns annually for several years; most salmon and eel migrate to their breeding grounds and spawn only once. The migrations of fishes for spawning are usually to situations where suitable conditions for the development of eggs and fry are found. There are apparently three conditions that influence the migratory movements of the spiny lobster: cold causing retreats into deep water, and molting or mating inducing movements toward shore (Crawford & Smidt 1922). The minnow, *Fundulus heteroclitus*, migrates into marshes in summer to secure food and live at high temperatures but returns to the ocean and remains near the mouths of rivers during the winter. During favorable seasons it wanders back and forth between the ocean and freshwater (Chidester 1920). The West Indian whitebait, *Sicydium plumieri*, lives in mountain streams but in the dry season migrates to the sea, spawns, and dies (Clark 1905). The young ascend streams again

in the rainy season. This fish will live for several hours, exposed in the sun, if pools dry up.

Control of Migrations.—On the whole, changing temperatures and food supplies exercise a general control over the migrations of animals, but they are not necessarily the direct or indirect causes of migratory movements. Sherman (1910) observed that during a mild spring birds nested earlier but did not arrive earlier. Phillips (1913) even asserts that birds have a "time sense," because he found their dates of arrival during migrations so regular in succeeding years. On the other hand, Cooke (1911) makes it clear that the northerly movement of the robin each year is correlated closely with the attainment in any locality of a certain mean daily temperature. Coward (1912) maintains that, though there are numerous exceptions, the average of weather conditions does influence the average time of arrival of migratory birds in particular localities. Smith (1917) finds considerable correlation between the flights of night migrants and meteorological conditions. Adams (1909) also finds that bird migrants commonly arrive in "waves" following peculiar types of weather. Migratory fishes are known to be influenced by differences in temperature, and doubtless other factors are potent in setting their routes. The mackerel in the Black Sea were very sensitive to temperature variations, and a decrease caused them to move inshore (Galtsoff 1924). In this instance variations in salinity appeared to exert little influence. Powers (1923) observed that carbon dioxide tension was an important factor in the movements of the Pacific herring, this fish frequenting areas where the pH was between 7.76 and 7.73.

Methods of Migrating.—The methods of migration vary greatly among different species of animals. Some birds make a leisurely journey, feeding as they go, and food supplies appear to influence their routes; others make a direct and hurried flight, feeding little or not at all. Some birds (warblers) fly mostly at night during migrations; others (swallows) move by day. The migration routes of some species of birds are broad, and those of others are narrow paths. Different groups of birds of the same species may travel by different routes. Salmon hatched near the headwaters of rivers may move to the ocean after 6 months, and other young of the same species may remain in freshwater for 18 months. The sea-run salmon probably often remain near

the mouths of the rivers where they hatched (Cobb 1921) and even come into the rivers to feed (Rich 1920). After spending 2–7 years in the ocean, salmon migrate up rivers, fasting and maintaining their energy from reserves of fat stored in their bodies. There is an increasing body of evidence that each race of salmon

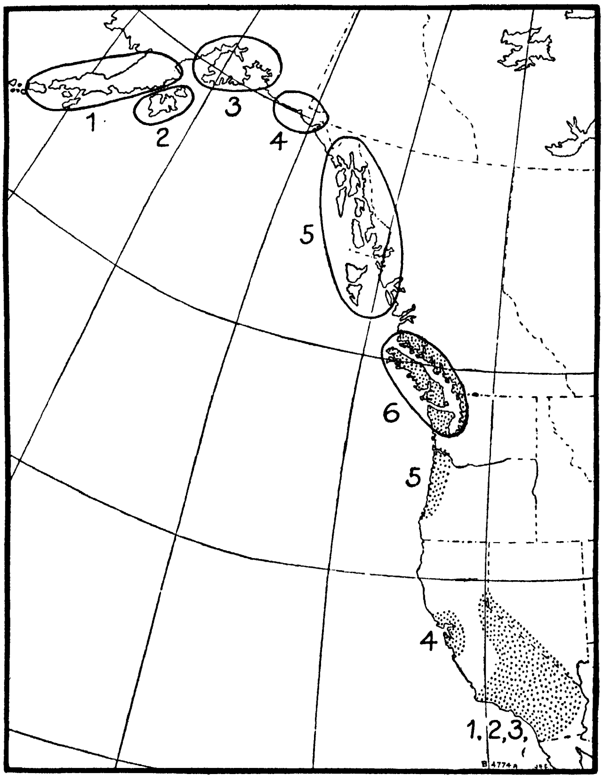


Fig. 38.—Migrations of Pacific-coast races of the fox sparrow. The breeding ranges are enclosed with solid lines; the winter ranges are dotted. The races at the extremes of the geographic range make the longest migrations; those near the middle migrate little (5) or not at all (6). (*From Lincoln* 1935, *after Swarth.*)

returns to breed in the river in which it hatched (Davidson 1937, Rich 1935, 1937), but Huntsman (1937) cites instances in which this is not so. There is also evidence that schools of migratory fishes retain a considerable degree of continuity, often for several years (McKenzie 1934, Schroeder 1930, Thompson 1933). Some species of birds are migratory or not as environment changes and appear to be able readily to assume or give up

habits of migration (Grinnell 1931). Prince (1920) suggests that such fishes as salmon have continued to go back to gravel beaches that were originally on the seashore but have gradually migrated inland with the development of rivers. Southwell (1905) maintains that the races of mackerel remain distinct. Those that hatch on a particular spawning ground swim together in a school, which maintains its identity for years. Along the Atlantic coast of America cod travel along rather definite routes to and from shore (Smith 1912). Among many species of animals (fishes, birds, seals) the males generally precede the females on the migration to the breeding grounds and often protect certain areas while awaiting the arrival of their mates.

Pathfinding.—The means by which birds and fishes find their way to the spot where nesting or spawning is to take place have excited much speculation. There have been more or less superstitious advocates of "instinct," magnetism, semicircular canals, "sixth" senses, and other rather unscientific explanations. Birds certainly have a homing instinct, and many individuals of many species are known to return to the same spot year after year to breed. Certain fishes migrate to particular breeding areas. How birds find their way during migrations is still somewhat of a mystery, though some are known to follow coast lines, to make use of landmarks, in certain cases to follow leaders to some extent, and to receive more or less aid from favorable winds. Other species strike off across open tracts of ocean (Fig. 36) and find their way without landmarks (Lincoln 1935). Some birds migrate by day, others at night, and some by both or either. Ward (1921, 1928) affirms that the red salmon in migrating up the Yukon River chooses the coolest water at each fork; but, according to Huntsman (1920), Roule maintains that the amount of oxygen in the water is the primary factor in determining which branch of a stream salmon ascend.

Extent of Migrations.—The extent of animal migrations varies within wide limits. Douglas (1917) divides the woodcock of Ireland into three groups: (1) resident birds which remain for several years in the general region where they hatched, (2) birds that migrate south, and (3) those that come from the north to spend the winter. Coward (1912) classifies all birds as follows: (1) permanent residents, (2) summer residents, (3) winter residents, (4) birds of passage which are in localities where this name

would apply for only a short time as they pass back and forth between breeding and feeding grounds, (5) irregular migrants, (6) stragglers. The golden plover travels about 15,000 miles each year, and the arctic tern about 22,000 miles. The European eel (Schmidt 1922) spawns in a rather limited area north of the West Indies, and the larvae during three years travel over a quarter of the earth's surface in order that adult eels may inhabit favorable habitats from the Nile to the regions about the Baltic Sea. In 1917 in Wood River, Alaska, 1,081,378 red salmon passed upstream to spawn; these were accompanied by about 100 humpback salmon and 30 king salmon. Some animals move very short distances during their annual migrations. The brackish-water snail, Ilyanassa, makes a journey of 5 to 60 yd. downstream in autumn, hibernating in deep water, and returns upstream again about the middle of April (Batcheler 1915).

Speed of Migrations.—Migrating birds attain altitudes of 20,000 ft. but usually travel at 1,400–5,400 ft. or less above the earth (Coward 1912, Lincoln 1935). Birds in active flight attain speeds of 50 to more than 100 miles per hour (Cooke 1937), but most species migrate 30–200 miles per day. The American robin takes 90 days to make about the same journey that the blackpoll warbler accomplishes in 30 days (Cooke 1911). The king salmon moved 62 miles per day for 13 days and on its whole journey traveled 1,500 miles at an average of 42 miles per day. The sockeye salmon in the Frazier River averages 10 to 17 miles per day for 470 miles (Gilbert 1922). This species apparently shows no retardation in speed in moving from salt into fresh water (O'Malley & Rich 1919). The chinook salmon moves upstream at a rate of 15 miles per day. A cod has been known to move at the rate of 16.5 miles per day (Smith 1912). A spiny lobster off the California coast traveled 6 miles in 14 days, but all the individuals observed averaged 1.4 miles during 22 days (Allen 1912).

DORMANCY

Types of Resting States.—Hibernation and estivation are resting states during which animals exist in a more or less torpid condition. The former is usually associated with cold, but many animals become inactive at particular seasons or at certain

periods in their life cycles, even when the temperature remains high. Estivation is usually associated with warm, dry periods and is characteristic of many tropical animals, particularly in localities where there are sharply defined rainy and dry seasons. Encystment is a resting state within a more or less impervious capsule, or cyst wall. It enables many animals to survive when environment fluctuates beyond their limits of toleration. It is characteristic of protozoans, rotifers, annelids, molluscs, crustaceans, and certain stages of various parasites, especially flatworms and nematodes, while resting within hosts. In some cases resting states are alternatives to migration—when animals are unable or are disinclined to move to a more favorable locality where they may remain active. In other cases they appear to be assumed when conditions are favorable for continued activity and are therefore to be looked upon as the result of desire or necessity for rest which is due to causes within an animal itself (Heape 1931). The environmental conditions that are most often associated with the assumption of resting states by animals are lack of food, low temperature, and drought.

Hibernators.—Throughout the animal kingdom there are hibernators. It is natural that, after a period of intense activity when food and energy have been utilized to produce offspring, animals should go into a resting state while the world is cold and unproductive. Hibernators usually occur in temperate, arctic, antaractic, and alpine regions. Many poikilothermic terrestrial animals (frogs, toads, insects, etc.) seek aquatic habitats or burrow in soil in winter. They thus attain a greater degree of environmental stability while torpid. On the other hand, some fishes remain active until actually frozen into solid blocks of ice; and many of them survive such freezing (Heape 1931). Some nongregarious types collect into groups for hibernation and give mutual protection. Social animals such as bees, though confined to their nests, feed and remain active enough to maintain their temperature above that of the environment. According to Folsom (1923), insects commonly hibernate (1) as adults, when they can deposit their eggs early in the following spring on proper food for their young; (2) as larvae, when they are protected from cold and are able to feed late in the autumn; and (3) as pupae or eggs, when nonfeeding, resistant stages are necessary on account of environmental conditions. Among mammals hibernation is

limited to representatives of the monotremes, insectivores, bats, rodents, and certain carnivores (Johnson 1931).

Estivators.—Where heat and drought are likely to interfere with the activities of animals or plants there are often estivators, especially in the tropics. At times terrestrial animals may go into long resting states during very wet periods. Hora (1925) describes a snail that remains quiescent during prolonged rains in a part of India where annual precipitation exceeds 400 in. He (1928) believes that habits of resting have been independently acquired there among various groups of snails in response to different environmental factors. Certain swamp-inhabiting fishes (Protopterus, Lepidosiren, etc.) can live in a torpid condition, encapsuled in cocoons of dried mud. The serpentheads (Ophiocephalidae) of the Indo-Malayan Region are famous for their ability to live for months buried in dry rice fields, and a native farmer "fishes" for them with a spade. Among reptiles there are noteworthy estivators among snakes, lizards, and tortoises. Perhaps the most remarkable examples among vertebrates are certain moist-skinned Australian frogs which become turgid and globular with water, then burrow and wait through periods of drought for another rain. In Australia also Tillyard (1917) has described dragonfly nymphs that remain alive for months in perfectly dry sand. They become so dry that their bodies crackle when touched but recover in a few minutes when placed in water. There are other estivators among insects (Buxton 1923), and other invertebrates.

Induction of Dormancy.—A dormant condition may be induced in an animal by various means. Among common causes starvation, low temperature, high temperature, desiccation, and obesity may be mentioned. Among mammals hibernation can be brought about more easily by starvation than by low temperature (Simpson 1912). Some mammals either become dormant or migrate when food fails (Carlier 1910). Many animals cease to feed when temperatures fall to a certain point; but mammals, unless they hibernate, increase heat production at low temperatures (Pike 1923). There are a few mammals that become torpid at low temperatures when food is available. In them there is a transfer of water from blood (Barbour 1921), and this doubtless slows metabolism. Rodents may delay their hibernation beyond the usual time if high temperatures obtain but, if

hibernating, may continue to do so at high temperatures (Cleghorn 1910). Some remain active until they become very fat and then go into a torpid state. Certain rodents may awaken at intervals during hibernation to void excreta and perhaps feed. Certain insects prepare for hibernation by losing water from their bodies (Tower 1907, Bodine 1922). Some of them then become dormant at rather regular intervals, without particular reference to environmental conditions; others are apparently thrown into resting states quite directly by environmental changes (Cousin 1932, Holmquist 1928, Morgan & Wilder 1936, Robaud 1934, Tuleschokov 1935). The cladoceran, *Moina macrocopa*, appears to produce two types of eggs, one of which rests for a time, the other developing at once (Wood 1932). It is possible that anaesthetic or hypnotic states at times play a part in bringing on dormancy (Buchanan 1923, Johnson 1930, Schmidt 1919). Many bottom animals in Lake Mendota remain dormant in oxygen-free water but at once become active if oxygen is supplied (Birge & Juday 1908, 1911). Some of these, however, become inactive before oxygen fails. Copepods in similar situations become dormant at very low or high temperatures (Coker 1934). In mammals hibernation is apparently not related to blood sugars as influenced by insulin (Dische, Fleischman, & Trevani 1931). There is no doubt that dormancy comes about from various causes, which differ in different animals and habitats.

Changes during Dormancy.—A dormant animal is not wholly inactive. It must use up its stored food reserves while its metabolism proceeds at a very slow rate (Van der Hyde 1921). A frog during hibernation loses fat and blood sugar, but its gonads develop, and its total water increases (Ott 1924, Suzuki 1935). Though torpid and inert, its metabolism is not stationary. A hibernating bee is so small that it can store comparatively little reserve food within itself but, if supplied with glucose at intervals, will live through a winter (Kalabukhov 1933, 1934). The bodies of bees are usually kept at rather high temperatures by exercise and the insulation furnished by the walls of their abodes. The temperature of a bee cluster may be 20–30°C. when temperatures outside vary between −9 and −11°C. (Phillips & Demuth 1914). Homeothermic animals become temporarily poikilothermic during hibernation (Eisentraut 1934, Johnson 1931), and their

tissues retain ability to respond for some time after being removed from their bodies (Cleghorn 1910). Hibernating mammals show heart block (Buchanan 1923) and a peculiar type of respiration in which a few rapid movements alternate with long breathless periods. They lose weight. Woodchucks lost 3.25 g. per kilogram during a dormant period of 110 days (Rasmussen 1917). Female skunks hibernate for longer periods than males and lose more weight, *e.g.*, 15 per cent, 40 per cent (Hamilton 1937). Hibernating insects can survive temperatures that would be fatal to those in an active state (Lozina-Lozinskii 1935, Payne 1926). Animals commonly lose water from their bodies in preparation for dormancy, and water increases rapidly when activity is resumed. An insect's resistance to minimal temperatures is increased in proportion to the degree of desiccation that its body shows (Bodine 1922). One way to break up hibernation in insects is to supply water (Townsend 1926). Endocrine glands are not believed generally to be concerned directly with hibernating states in mammals (Eisentraut 1934, Johnson 1928, 1929, 1930, 1931, Zalesky 1935), but Herter (1934) believes that they may be. The so-called hibernating gland has been investigated by Rasmussen (1923), who concludes that it is not a gland, as it secretes nothing. In a woodchuck it constitutes 3 per cent of body weight before hibernation and 0.75 per cent after. It contributes about a twenty-fifth of the substance lost and appears to be only a store of fat. In the bodies of certain animals (crabs, ascidians, brachiopods, crayfishes, molluscs) there is an increase in calcium content during winter, which is believed to give increased resistance to low temperatures. Molluscs in ponds can live in water without oxygen for considerable periods and use calcium in their shells for buffering acids (Dotterweich, Heinz, & Essner 1935). Blanchard and Blatin (1907) were unable to infest hibernating marmots with trypanosomes, spirochetes, or trichinae, probably on account of low body temperatures. Animals when ready to hibernate usually choose a retreat where, though perhaps very cold, they will be protected from actual freezing. Their torpid condition makes them helpless. Frogs, salamanders, and toads go into springs and ponds or burrow below frost line; bears and bats resort to caves and hollow trees.

Duration of Dormancy.—The dormant states of animals may continue for years. Semper (1881) kept some land snails in

paper for 3 years and found them alive when unwrapped. He states also that trichina cysts remained alive in flesh for 10 years. Van Beneden (1876) observed that tapeworm cysts remained alive for years. Bodine (1923) found Colpoda cysts alive after 3 years and kept cysts in a desiccator for 6 months without killing them. He states that the resistance of such cysts to cold and chemicals is proportional to the degree of desiccation that they have undergone. The cysts of Didinium were viable after a rest of 5 years (Mast 1917*a*), and flagellates have been reared from dried sediment that had been sealed for 20 years (Hausman 1934). Shaw (1925) has studied the estivation and hibernation of the columbian ground squirrel. He says:

> It has long been known that a regular order of sex precedence exists among migratory birds. That a corresponding precedence should exist among aestivating and hibernating mammals is not surprising. . . . Adult male squirrels were the last to go into aestivation, and the first to come from hibernation. Adult males were from four to six days later in going to aestivation than adult females; and were from seven to fifteen days earlier in returning from hibernation. The average duration of hibernation for adult males was 204 days, and that for the adult female was 220 days, or a difference of sixteen days. The longest hibernation period was that of a young female, 238 days.

Another remarkable ground squirrel (Cynomys) lives in the deserts of Turkestan. It is active only 3.5–4 months when there is green vegetation and is lethargic during the remainder of each year. Its summer estivation period continues into a winter hibernation. If supplied with food and water, it will remain active until December before it hibernates (Kashkarov & Lein 1927).

Functions of Encystment.—Encystment is one means by which many animals are able to increase their chances of survival when the environment fluctuates beyond their normal limits of toleration. Colpoda cysts are better able to endure gradual than sudden changes in temperature or the chemical constitution of the surrounding medium (Bodine 1923). The more cysts are desiccated the greater is their resistance. In cultures of Didinium conjugation is usually accompanied by encystment, and Mast (1912) therefore concluded that either process might be of service in preparing for an unfavorable period. Hopkins (1921) asserts that encystment restores the power of conjugation to

rundown strains of Paramecium. Mast (1917*a*) was able to make Didinia encyst at any time, by cutting off their food supply, but he also observed that they often encysted when food was plenty. These protozoans could be induced to emerge from their cysts by adding Paramecia (their usual food), or even a filtered extract from a Paramecium culture, to the medium containing them. Mast concluded that encystment served to carry Didinium over unfavorable periods and as a favorable state for distribution to new habitats, particularly when cysts were dry. He found that ex-conjugants often became encysted but could not become so unless food was available. In later studies Mast and Ibara (1923) discovered that Didinium encysts most often at temperatures between 25 and 30°C., which are also the range of the optimum for growth and fission, and that it does not encyst at injurious temperatures, low or high. They found that there is most encystment when most food is present and believe that it is probably brought about by the presence of waste products. Though it is a protection from starvation and supra- and suboptimum temperatures, it is not necessarily directly induced by such conditions. Recently Beers (1927, 1928, 1930, 1931) has made further studies on Didinium. He finds that encystment is induced by absence or poor quality of food and by excretory products but that a Didinium will not encyst unless its own body contains a certain amount of food. "Encystment in Didinium may function to increase the vitality of the race when the animals are depressed by inadequate cultural conditions," but such increase is probably not due to a rejuvenating process in this case (Beers 1930).

TROPICAL REGIONS

Characteristics of Tropics.—The regions of the earth from the equator to the limits of mean annual isotherms of 20°C. (68°F.) have tropical climates. High temperatures characteristic of the tropics are due to the altitude of the sun, the high temperature of soil, and the presence of water vapor. Water not only serves as a transparent thermal blanket which allows radiant energy from the sun to pass through to the earth but also absorbs heat that is lost from soil and at night, by condensation into dew, gives up heat so that air and soil temperatures are maintained. The warm surface of the tropical ocean continually supplies moisture

to the atmosphere, and warm winds help in keeping temperatures uniform. However, tropical climates are not always monotonous. Where there is little moisture, "night is the winter of the tropics" (Visher 1923). Thunder showers serve to cool the atmosphere and cleanse the soil. In many localities they occur daily with great regularity. In his "Naturalist on the River Amazon" Bates (1892) gives a description of:

A Typical Tropical Day.—At that early period of the day [the first two hours after sunrise] the sky was invariably cloudless, the thermometer marking 72° or 73° Fahr.; the heavy dew or the previous night's rain, which lay on the moist foliage, becoming quickly dissipated by the glowing sun, which, rising straight out of the east, mounted rapidly towards the zenith. All nature was fresh, new leaf and flower-buds expanding rapidly. . . . The heat increased hourly, and towards two o'clock reached 92° to 93° Fahr., by which time every voice of bird and mammal was hushed. The leaves, which were so moist and fresh in early morning, now became lax and drooping, and flowers shed their petals. On most days in June and July a heavy shower would fall some time in the afternoon, producing a most welcome coolness. The approach of the rain-clouds was after a uniform fashion very interesting to observe. First, the cool sea-breeze which had commenced to blow about ten o'clock, and which had increased in force with the increasing power of the sun, would flag, and finally die away. The heat and electric tension of the atmosphere would then become almost insupportable. Languor and uneasiness would seize on every one, even the denizens of the forest betraying it by their motions. White clouds would appear in the east and gather into cumuli, with an increasing blackness along their lower portions. The whole eastern horizon would become almost suddenly black, and this would spread upwards, the sun at length becoming obscured. Then the rush of a mighty wind is heard through the forest, swaying the tree-tops; a vivid flash of lightning bursts forth, then a crash of thunder, and down streams the deluging rain. Such storms soon cease leaving bluish-black motionless clouds in the sky until night. Meantime all nature is refreshed; but heaps of flower-petals and fallen leaves are seen under the trees. Towards evening life revives again, and the ringing uproar is resumed from bush and tree. The following morning the sun again rises in a cloudless sky; and so the cycle is completed; spring, summer, and autumn, as it were in one tropical day. The days are more or less like this throughout the year. A little difference exists between the dry and wet seasons; but generally the dry season, which lasts from July to December, is varied with showers, and the wet, from January to June, with sunny days. It

results from this, that the periodical phenomena of plants and animals do not take place at about the same time in all species, or in the individuals of any given species, as they do in temperate countries. In Europe a woodland scene has its spring, its summer, its autumnal, and its winter aspects. In the equatorial forests the aspect is the same or nearly so every day in the year; budding, flowering, fruiting, and leaf-shedding are always going on in one species or other. It is never either spring, summer, or autumn, but each day is a combination of all three. With the day and night always of equal length, the atmospheric disturbances of each day neutralising themselves before each succeeding morn; with the sun in its course proceeding midway across the sky, and the daily temperature almost the same throughout the year—how grand in its perfect equilibrium and simplicity is the march of Nature under the equator!

Tropical Season Rhythms.—In the tropics there is usually no time of year when plants and animals are generally resting, except in regions where there are well-defined rainy and dry seasons. Therefore there are less striking seasonal rhythms than obtain in temperate and frigid regions. The abundance and variety of life are due to the general uniformity and permanence of favorable conditions. Radiant energy from the sun is evenly distributed throughout the year and, unless there is drought, photosynthesis can supply basic foodstuffs at a uniform rate. Tropical forests do not wholly lack periodicity that is more or less correlated with seasonal changes. Indeed, some tropical forests are not evergreen; but, in general, there is no time when vegetation is not actively at work, and some plants shed their leaves only at intervals of several years. Tropical lakes often show only one annual "overturn," when temperatures become uniform from top to bottom, instead of two, which is characteristic of lakes in temperate climates (Juday 1915). Birds may nest and lay eggs at definite seasons or have long breeding periods which extend through most of the year (Moreau 1936, Sody 1927, Van Tyne 1929). Certain invertebrates and vertebrates show lack of seasonal rhythms. In Malay carp introduced from China may spawn ten times during a year and attain sexual maturity at the age of six months (Buschkiel 1932).

Tropical Biota Is Varied.—Tropical faunas and floras present great variety. A typical rain forest does not consist of a few dominant species of trees, as do forests in temperate regions,

but of many types which struggle with each other for room to spread their leaves beneath the sun. A traveler plodding along a trail notices a peculiar tree and perhaps walks half a mile before he sees another of the same species. Aquatic habitats of limited extent are often deficient in oxygen, because temperatures are high and life is abundant. Such conditions have doubtless been a factor in the evolutionary changes that have led to the extension of branchial respiratory surfaces (Hora



FIG. 39.—A goby, *Periophthalmus kohlreuteri*, which climbs about on the roots of mangroves in Nigeria.

1936) or transformed branchiate to pulmonate animals (Pearse 1936). In a dense rain forest shade may be so deep that some animals resort to treetops. In the tropics there are many transitional forms which are changing, or have recently changed, from one habitat to another. There are land planarians, river crabs, land crabs, tree-climbing fishes (Fig. 39), flying lizards, giant snakes, gaudy birds (Fig. 40), and other peculiar forms that are rare or absent elsewhere. Further information about some of these is given in Chapter X.

Productivity of Tropics.—With continual high temperatures and rather uniform light conditions throughout each year, it might perhaps be expected that the tropics would produce an abundance of life, but this expectation is not always fulfilled. The cold oceans produce more plankton than those in the tropics and support extensive fishery industries. Attached marine algae are small and insignificant compared to giants that often

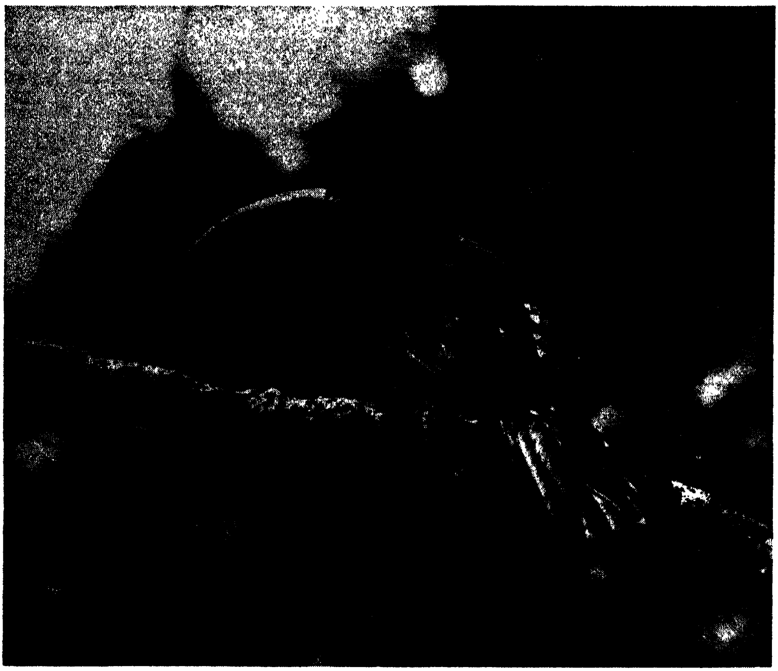


FIG. 40.—A toucan, *Ramphastos brevicarinatus*, which is a common bird in forests in Central America. (*After Van Tyne* 1929.)

grow along chilly, rock-bound coasts. Perhaps large amounts of radiant energy kill feeble plants like plankton algae (Woodruff 1910). Bacteria are often abundant and doubtless remove nitrogenous materials, but there is little evidence that they precipitate lime (Lipman 1931). The great lime deposits are in warm seas. They are due to the activities of corals, worms, and other animals and algae. Tropical deserts result from heat and light without water. Such barren wastes support little life. But on freshwater and humid land areas, tropical animals



FIG. 41.—Fungus bed of a leaf-cutter ant, Colombia.



FIG. 42.—Rubber trees and toddy palms, Nigeria.

may flourish in great numbers. There are many that are peculiar to warm climates. Though there are many of them that are active in bright sunlight, the number of crepuscular and nocturnal types is strikingly large. An animal that hides in the shade or hunts at night may take advantage of the food produced by great photosynthetic activity in a tropical forest but avoid the injurious effects of light and heat. The tropics furnish many valuable products to man (rubber, timber, cacao, copra, palm oil, coffee, etc.), and these have been exploited by races that evolved in temperate climates (Fig. 42). Some believe that white men will never be able to live permanently in the tropics (Nicoll 1918), but who knows what air-conditioned buildings and other inventions may make possible in the future?

ARCTIC AND ANTARCTIC REGIONS

Frigid Regions.—The north and south frigid regions of the earth have much in common, yet each has characteristic plants and animals and especially on land presents quite a different aspect. Both have low temperatures throughout each year, long periods of day and night near the poles, and an essential aridity in land and freshwater habitats, because there is a lack of available moisture for plant growth, though fresh water in the form of snow and ice is abundant. There is much more life in polar oceans than in land and freshwater habitats. There have been advocates (Pfeffer 1901, Allgen 1934) and opponents (Ortmann 1899) of the theory of "bipolarity," *i.e.*, that animals in the two frigid regions of the earth are related. There is no evidence for this among land and freshwater plants and animals, but some species in the ocean are alike. The arctic marine biotic areas are more clearly defined than those in the antarctic (Broch 1933). The line where the annual mean of 0°C. occurs separates boreal and arctic faunas rather sharply, but pelagic animals are not so definitely distinguished.

Food Resources in Cold Regions.—As plants are essential, directly or indirectly, for animal foods, the food on land and in freshwater is very limited; but the diatoms, seaweeds, and other marine plants support an abundant fauna in the oceans. Some essentially marine animals, such as seals and sea birds, resort to land only for resting or safe breeding places. Cold oceans have more plant and animal life than those in the tropics.

This may be due to (1) retardation of metabolism by low temperatures so that each individual lives longer, (2) the greater abundance in tropical seas of bacteria and other nitrogen-using organisms which deplete food resources, and (3) the greater capacity of cold waters to hold gases in solution. Many animals that spend all or much of their lives on land are dependent on the sea for food. A polar bear eats considerable amounts of grass and seaweed (Koettlitz 1900). The length of its intestine is remarkable (180 ft.), being twenty-two times that of the body. Polar Eskimos flourish on a diet that contains little or no plant



FIG. 43.—A lemming, *Dicrostonyx torquatus*, which lives in Novaya Zemlya. (*From Økland* 1928.)

food. Even typically terrestrial animals, such as weasels, foxes, and wolves, forage along the seashore, but they also prey upon vegetarian land animals—caribou, musk oxen, hares, and lemmings (Fig. 43). Birds in frigid regions get their food largely from the ocean, but there are a few scavengers and robbers (skua gull, raven) and predators on land animals (snowy owl). In the ocean there are the usual food chains: from diatoms through copepods and schizopods to whales, from seaweeds to molluscs through fishes to seals (Gray 1931).

Care of Young.—The young of arctic animals are usually attended with great care. A polar-bear cub, though foraging for itself more or less, remains with its mother and is suckled for 2 years. Penguins escape their chief enemy, the sea leopard, by marching inland to rookeries on windswept barrens where loose stones are available for nests (Fig. 44). There is great

rivalry for building material, and the female Adelie guards the nest while the male collects stones. The parents fast for as much as 27 days while mating, building the nest, and beginning the incubation of eggs. The male and female then take turns at fishing, and the young feed themselves from their parents' crops (Fig. 45). Levick (1914) determined the rate of growth of the young, and found that there was an increase from 3 to 42.5 oz. during the first 12 days after hatching. A couple of

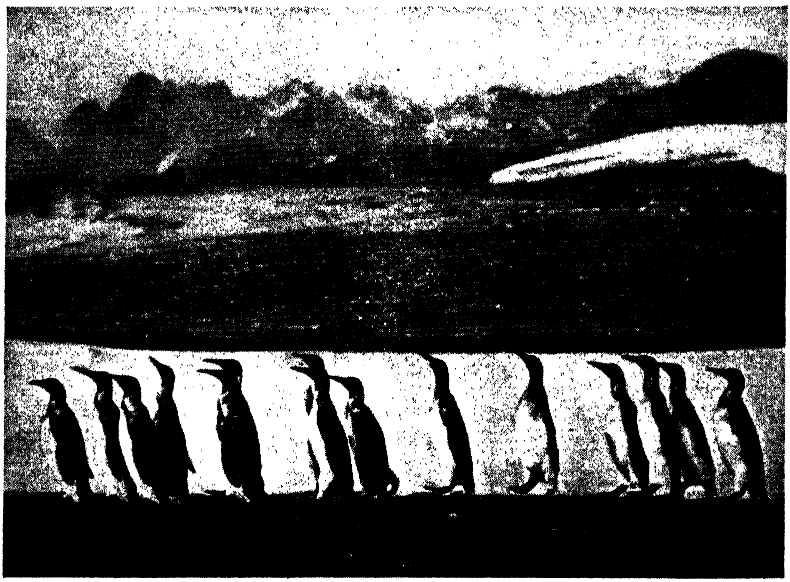


FIG. 44.—King penguins marching to the sea, South Georgia. (*From Murphy* 1915.)

weeks later the young are herded together and attended by a few adults, while unoccupied members of a colony feed and play in the ocean. The emperor penguin lays its single egg in the dead of winter, and the parents take turns holding it to keep it warm. This species molts in a hole in the snow, where it remains for more than 2 weeks. Jourdain (1913) has observed that passerine birds in Iceland lay larger clutches of eggs than those in England. Seals and sea birds commonly resort to isolated islands and inaccessible cliffs to rear their young.

Adaptations of Animals in Frigid Regions.—Outside the ocean the arctic and antarctic faunas consist of a comparatively small number of highly specialized species which show unusual adjust-

ments to the rigorous environment. A number of birds and mammals (bunting, ptarmigan, hare, ermine, etc.) shed their coats twice a year, so that they are white in winter and pigmented in summer. The accumulation of fat for insulation and storage is common in the bodies of animals. Many animals are able to withstand inanition for considerable periods of time. Arctic Diptera are covered with heavy coats of bristles. Certain of the mammals, birds, and fishes make seasonal migrations. A caribou's hoof has a very wide expanse, so that it does not readily sink into snow; its frog is resorbed during the winter, and



FIG. 45.—A young Adelie penguin feeding from its parent's crop. (*From Gain* 1913.)

the sharp edge then prevents slipping on ice. Penguins are covered with a thick layer of fat, can dive and feed under water with great skill, and have peculiar social instincts which are important for their survival. Thirty-six species of birds live south of 60°S. (Gain 1913). All these live in or near the sea and are dependent upon it for food. The five species of penguins show a high degree of specialization for life in the Antarctic Ocean. A penguin cannot fly but uses its front limbs for swimming. It is perfectly at home in the water, being able to dive to a depth of 50 ft.; its food consists largely of fishes and pelagic crustaceans. The absence of such predators as foxes and bears in the antarctic makes it possible for penguins to breed on land.

Arctic birds are all able to fly and usually resort to inaccessible cliffs or islands to breed (Gorbunor 1932).

Marine Animals.—Cold seas often teem with life, especially types that live on the bottom or float in open waters. Echinoderms, molluscs, worms, and crustaceans are among the most abundant small invertebrates. Well known among larger animals are squids, various fishes, walrus, seals, narwals, and whales. The character of faunas in arctic coastal bays and fjords (Stephensen 1916) depends on connections with boreal or arctic oceans.

Freshwater Animals.—The arctic freshwater fauna is rather limited in species, but at times abundant in particular situations during the brief summer season. Protozoa, cladocerans, fairy shrimps, amphipods, rotifers, midges, and mosquitoes develop in pools. Caddis-flies and May flies are found in flowing streams. In Canada mosquitoes are unbearable for 10 weeks on the arctic barrens but are abundant for only about 8 weeks in the spruce forest and for 6 or 7 weeks in the wheat belt.

Land Animals.—Except for animals that depend on the ocean for food, the land animals of arctic and antarctic regions are not abundant. The arctic "barrens," however, support a considerable number of animals. The ice floes are the resorts for the seal, walrus, and polar bear. Stefansson (1922) resents the notion that many persons hold regarding the dearth of life in the arctic:

> To sum up, the arctic sea is lifeless, except that it contains about as much life to the cubic mile of water as any other sea. The arctic land is lifeless except for millions of caribou and of foxes, tens of thousands of wolves and musk oxen, thousands of polar bears, billions of insects and millions of birds. And all these go south in the fall except the insects which die as they do in temperate lands, and except the ptarmigan, caribou, foxes, wolves, musk oxen, polar bears, lemmings, hares, weasels, owls, and ravens, all of which we have named in approximately the order of their decreasing numerical strength.

Insect visits to plants are rare in the arctic; anemophily and autogamy are common (Schimper 1903). True bulbs and tubers are rare; many arctic plants have dwarf, prostrate, or rosette habits of growth. Most plants are perennials (Warming 1909) and flowers and fruits are therefore commonly formed before the short growing period and appear very quickly when the

favorable season arrives. Viviparity and vegetative reproduction are often observed among arctic plants. A "plankton," which consists of algae, podurans, tardigrades, oligochetes, and nematodes, may occur in snow. Johansen (1921) found that land insects decreased rapidly in numbers as he went north in Canada. Forest insects dropped out first; scavengers and predaceous species extended farthest north. Mites and a few spiders persisted as far as land extended. Phytophagous species are rare, but bloodsuckers and scavengers may be abundant at times. Caribou move north in summer to avoid these pests (Seton 1911). Arctic regions are invaded in summer by many migratory birds, especially plovers, snipe, ducks, and geese. Some small birds, such as the snow bunting, also breed there. There are few soil animals (Anderson & Falk 1935), but they do occur in favorable situations where ground thaws in summer; in Greenland, Jorgensen (1934) found nematodes, insects, spiders, and mites in soil. The Antarctic Continent, which is now much smaller than during the past, has a very limited invertebrate fauna but supports isopods, collembolans, and mosses which show affinities with New Zealand and South America (Chilton 1909). The flora on land in the antarctic is nearly nonexistent. There are a few algae, lichens, and mosses.

ALPINE REGIONS

Alpine Conditions and Animals.—Arctic and alpine regions have some things in common, though arctic food resources are largely in the sea, whereas those at great altitudes come from lower levels or are produced locally. In alpine regions the mean annual temperature is not so important in relation to life as the degree of warmth during, and the length of, the summer season. Such regions throughout the world have similar faunas which consist of (1) true alpine animals, like the lemming, chamois, and mountain goat, which are not found in the lowlands but may have relationships with the animals of polar regions, and (2) ubiquitous species which usually have a wide range and have invaded alpine regions since glacial times. The temperature in all alpine habitats is always low, and food resources, as represented by plants, are not produced rapidly. In general, there is a period of renewed activity and multiplication at the time when snow melts. On account of the scarcity of food and continual low temperatures,

dwarfs are common. There is a tendency to the prolongation of life, because animals are active for such a short time each year. Many poikilothermal animals are viviparous. The gestation period of the alpine salamander is 3–4 years; the eggs of crustaceans develop slowly and may winter over before hatching (Schultz 1912). Hesse (1921) states that the eggs of alpine animals are often laid in sunny places, whereas comparable animals in the tropics usually deposit their eggs in shade; also, that the bodies of alpine animals contain and require less water than those of animals in the tropics. The size of the heart is large, and respiratory capacity is comparatively high in alpine land vertebrates.

As in the polar regions, annual plants are rare in the alpine zones. Lakes are free from ice for only two or three months out of each year, and their temperatures are seldom above freezing. Yet they have a characteristic, though scanty, fauna. Dodds (1917) observed that alpine species of plankton crustaceans, like *Diaptomus shoshone* Forbes, did not become established in mountain or lowland lakes, though they were constantly carried into them by streams. Sarcodinans persist in lakes at higher altitudes than do other protozoans (Edmondson 1912). Steinmann (1908) has given an excellent account of the animals in alpine brooks, which maintain a low and more or less constant temperature throughout the year. The commoner brook animals in the Alps are amphipods, May flies, caddis-flies, mites, leeches, and planarians. The land animals in alpine regions are highly adapted to stand exposure, and some of them migrate to lower levels or latitudes during the coldest weather. Schimper (1903) noted that bees and bee-fertilized flowers decreased at higher altitudes and that there was a corresponding increase in Lepidoptera and the flowers pollinated by them. Alpine animals in temperate zones may be relicts or be derived from adjacent lowlands, but those in the tropics are usually derived altogether from neighboring regions (Gadow 1913). In the European Alps present distribution of certain animals is correlated with glaciation in the past (Heberdey 1933). A part of the food of alpine animals is derived from animals that wander upward from the lowlands and perish. Caudell (1903) identified 78 species of insects from a snowbank on Pike's Peak, and he stated that most of these apparently came from levels below.

SOLAR RHYTHMS

Sunspot Cycles.—Evidence has already been presented (pp. 5–6) that shows that radiant energy from the sun varies in amount through a cycle of about 11.3 years. Hurricanes on the sun appear on the earth as sunspots. On the earth, as energy received from the sun varies periodically, there are proportionate variations in plant growth (Fig. 2), rainfall, storms, radio reception, and other phenomena.

Solar Rhythms and Animal Populations.—Animals vary in numbers in any locality from year to year, and many observers have recorded 2-, 3-, 4-, 6-, 11-, 17- and 33-year cycles of abundance which have recurred with more or less regularity. Some of these are apparently due to inherent reproductive capacities in animals, to accidental favorable and unfavorable environmental conditions, to epidemics of disease, and to other causes. Some of them appear to be definitely correlated with periodic variations in solar radiation, which influence animals directly or indirectly. The numerical variations of certain fur-bearing animals and rodents (Shelford 1929), birds (Gross 1931), crop-destroying insect pests (Headlee 1934, Uichanco 1936, Wall 1932), and other animals apparently keep pace with sunspot cycles. Those of others (lemming 3.6 years) vary in shorter cycles (Shelford 1929) or through much longer periods (elephant 50 years, Elton 1927). In North America and Europe grouse fluctuate in 11-year cycles, but the periods in the two continents are not synchronous, and Leopold and Ball (1931) therefore conclude that such cycles are not due primarily to variations in solar radiation.

CHAPTER VII

COMMUNITIES, COMPETITION, POPULATIONS, AND CLASSIFICATION OF COMMUNITIES

COMMUNITIES

Character of Communities.—Communities are more or less complex groups of plants and animals that occupy particular areas. Every community is in a state of dynamic equilibrium and depends for its character and continuance on (1) the physical environment in which it exists, (2) the plants and animals that give life to it, and (3) interactions between environment and biota. From one point of view a biome is a space occupied, number of organisms present, and interactions. There are always binding forces in a community that tend to hold it together—food resources, food chains, cooperation, division of labor, etc. A community is in a sense a complex organism in that the whole is perhaps more than and different from a sum of all its parts (Clements 1935). Many ecologists usually study a community by counting the plants and animals in it. They use quadrats, transects, and other means for gaining knowledge of the number of each species present in a biome and how long each is present. They then arrange species as dominants, codominants, subdominants, influents, etc. (Clements 1935, Newcombe 1935). Such students have concluded that plants are dominant on land and that animals are dominant in aquatic habitats because they naturally count large and obvious things, even when they count under a microscope. They often lose sight of the fact that a numerous species that they name predominant is no more necessary in maintaining the stability of a particular biome than some less numerous plant or animal that is relegated to a lowly position as an influent or secondary "form." They worship the numerical fetish and feel that, the more statistical a body of data the better it is. There are other ecologists who, while respecting statistical procedures, feel that plants and animals should not only be counted but arranged in communities according to adaptations, life histories, and abilities to make

adjustments to characteristic and easily recognized environments. It is perhaps as scientific, and certainly more interesting, to discuss the animals of a swamp, rather than those of Typha-Juncus-Limnaea-Libellula biome. A dominant plant or animal is not necessarily the most numerous species in a habitat. Dominant species are those which exert controlling influence on environment.

Origin of Communities.—Communities as they are found on the earth are often climaxes which have come into existence through ecological succession, but there are always many that are still in a successional state. Communities usually change rapidly in early stages and more slowly as they approach a climax. A species in a preclimax may hold a dominant position but become unimportant in a climax. So communities progress or retrogress (Tansley 1935) and in a climax are ever in a state of dynamic equilibrium, like a complex organism. Elton (1927) points out that there are four basic factors in forming and maintaining communities: (1) food chains (animals generally tend to become larger and larger); (2) size of food (this influences the character of food chains); (3) niches (that which animals do, not what they look like, determines their status in relation to foods and enemies); and (4) pyramid of numbers (there are many, small, rapidly increasing animals at the base of a food chain, and few at the top).

Terminology for Communities.—There has been, and is, much confusion in the use of terms applied to communities as active groups of plants and animals. Recently Clements and Shelford (Newcombe 1935) have attempted to clarify the situation but with doubtful success. They propose (Clements 1935) to extend the use of "family" so as to make it even looser and vaguer than it now is and coin some new terms (*ece*, etc.) which seem to be unnecessary. They use dominants, subdominants, influents, subinfluents, and secondary forms for groups of decreasing "influence" in communities. Their use of "biotic community" is clear as "an assemblage of relatively uniform taxonomic composition and physiognomy" (Newcombe 1935). To the writer it seems to be ill-advised to base ecological communities on species and numbers. Usually such a viewpoint actually involves naming communities for genera, which commonly contain several species with various habitat preferences, and therefore becomes

vague and misleading. It is often difficult to determine which organisms exert "controlling influences." A disciple of Shelford's (Newcombe 1935) writes a paper entitled "Certain Environmental Factors of a Sand Beach in the St. Andrews Region, New Brunswick, with a Preliminary Designation of the Intertidal Communities"; and his principal community is "the Balanus-Littorina-Fucus biome." None of the three genera he has listed lives on *sand.* Obviously he is thinking more of species (or genera) and numbers than of habitats and biotic adjustments. Such terminology tends to become technical and meaningless, like the astrological jargon of the Middle Ages. The designation of communities with hyphenated generic names is objectionable not only because genera are usually multispecific but because they mean nothing to one who does not know local conditions. A native of Japan understands little from a "*Balanus-Littorina-Fucus* biome" but readily comprehends what is meant by a "rock-beach biome" or a "hard-bottom biome." A prairie in Africa contains some birds that are similar to those in Nebraska, but they belong to quite different genera and families. "Prairie biome" means something to an African ornithologist, but he will have to do some searching to find what "Sturnella-Otocoris-Stipa-Poa biome" signifies. In the synopsis of communities at the end of this chapter the writer has tried to use names for communities that are readily understandable.

COMPETITION

Struggle for Existence.—Animals are racially always "between the devil and the deep sea." If they are taking an active part in the affairs of the world and struggling toward what perhaps may chance to be a better type of existence, they must carry on a continual fight and are often in danger of defeat or death; if they have found a quiet eddy in the slack waters of evolutionary currents and are enjoying more or less immunity from competition with other species, they cannot hold a dominant position among animals in general and, though perhaps secure and more or less at ease, can take little or no part in shaping biotic communities or evolutionary trends. A lion is strong, aggressive, keen of sense, quick and sure in its movements. It is well suited to fight for its place in the world. A tapeworm insidiously

sneaks into its host, soaks in predigested food, and lives secure from the vicissitudes of the outside world. It has very little power of perception, is denied the pleasure of ingesting food because it has no enteron, and is in other respects limited. It is a degenerate parasite. Yet it survives. Biologically it is not proper to say that a lion is better than a tapeworm. One survival is as good as another.

Competition.—Competition is in some respects most keen among individuals of the same species, because they need and strive for essentially the same things. Species within a genus are usually protected more or less from competition by differences in habits. In this connection Cabrera (1932) has formulated the principle that "related animal forms are incompatible, and their incompatibility is the more profound the more directly they are related." If an animal becomes adapted to new styles of living, it may be able to invade habitats where there are no competitors. Vestal (1914) has summarized the characteristics that may remove animals from competition as: (1) structural (the fossorial forelimbs of the mole enable it to live underground); (2) physiological (the clothes moth lives on keratin, which is indigestible for most animals); (3) psychological (one mouse prefers to live in the forest, another in the meadow); (4) biographical (a butterfly hunts by day, a moth at night); (5) numerical (two species that use practically the same resources cannot be so numerous as when there is only one). Animals compete for food, space, mates, and other things. Those which survive and dominate a habitat may be strong, numerous, develop quickly, be generally superior biologically, or excel competitors in other ways. On the other hand animals which dominate particular biomes may be biologically inferior to others that live with them, but are more successful because of some peculiar quality they possess. A species may survive because it is immune to a parasite that exterminates another. Animals of one sex often fight others of the same sex; pairs fight against pairs for territory (Howard 1920). Warming (1909) states the results of competition as: (1) the establishment of natural communities; (2) unceasing changing and adjustment; (3) the production of rare species because suitable habitats are not to be found, because a species is new in a locality, or because it is a relict; and (4) perhaps also the origin of species. He also says that

dominance depends upon: (1) ability to obtain a foothold, (2) hardihood or endurance, (3) capacity for assimilation or rate of development, (4) reproductive capacity, and (5) freedom from enemies.

POPULATIONS

Population Theories.—During the past decade or two there has been great interest in populations. Statistical and experimental studies have furnished data for mathematical analyses, and various theories have been formulated. Volterra (Chapman 1931, 1933) lays down three laws for the fluctuations in populations where two or more species compete: (1) Law of Periodic Cycles (rhythms are inherent in populations and depend on increase or decrease of initial conditions); (2) Law of Conservation of Averages (populations remain stable unless conditions change); and (3) Law of Disturbance of Averages (if a population is being destroyed by an outside agent, eaten animals tend to increase and eaters tend to decrease). Chapman (1931) has stressed biotic potential and environmental resistance as influences that determine populations. Environment may vary to such extremes that plants and animals are killed; it may lack essential foods; it may contain predatory animals which destroy. An organism must have capacity to multiply so that it can continue to exist in spite of environmental resistance. If conditions remain essentially stable, plants or animals usually increase rapidly after being introduced into an area; then more slowly; and finally the population reaches a more or less steady state which continues until conditions change again. Species tend to spread and thus invade unoccupied niches or compete with each other, but in any area come ultimately to a condition of dynamic equilibrium (Longley 1936). Some students of populations have approached problems somewhat from the point of view of actuaries. Pearl and Miner (1935), thinking in terms of graphs, describe "percentage deviations from mean duration of life" under three groups: (1) rectangular, where most individuals die at about the same time; (2) intermediate; and (3) diagonal, with an approximately constant death rate. They believe that five major factors are concerned in age distribution of death: (1) endogenous senescence (the wearing out of an organism through internal functioning); (2) exogenous senescence (wearing out

through adverse environment, infections, diseases, etc.); (3) genetic constitution; (4) rate of living; and (5) immediately lethal accidents. They arrange these as three variables: genetic constitution, activity, and environment. More extensive discussions of population problems will be found in the works of Elton (1927), Chapman (1931), and Pearl (1925).

Natural Populations.—There have been many counts and estimates of the number of animals present on particular areas of the earth. Often these have been made by the use of transects, quadrats, tags, bands, and other more or less accurate methods. Small animals in soil may reach thousands per acre or square foot (Jones 1937, Waksman 1932, Wolcott 1918). On the surface of the ground, animals have been estimated by routine catches in sweep nets (Beall 1935, Gray & Treolar 1933). An ant colony (Formica) may contain 100,000 or more individuals (Andrews 1929). Fishes have been estimated by observation during migrations and by quantitative catches. Perhaps bird populations have been as extensively studied as those in any group of animals. On open lands in Illinois, Forbes and Gross (1922) found the following numbers of birds per square mile: cereal-crop areas, 602; pasture meadow, 923; tree shrub, 3,111. During 14 years on a 15-acre tract in Ohio, Kendeigh and Baldwin (1937) recorded an annual average of 19.7 wrens. Many other instances of population density studies might be cited.

Fluctuations in Natural Populations.—There are some cyclical phenomena, such as hibernation and annual migrations, that may greatly change the number of active animals in a region at different seasons. Some species also fluctuate rather regularly over longer periods. There are also many known cases in which animals vary in number with irregular changes in climate and other factors. It is well known to fishermen, trappers, and hunters, who depend on natural production, that certain age groups of animals are abundant and successful. In a particular year many conditions are favorable; an unusually large number of a species may survive and continue for several years. Elton (1927) gives examples of populations that increased rapidly for several years and became very dense, then were depleted by epidemics. Crowding, or overpopulation, is conducive to the spread of epidemic diseases. Some animals limit their own increase by saturating an environment, so that competition for

food and space is increased to such a degree that all cannot survive. There are also compensatory fluctuations—a favorable season may produce an unusually large number of predators; these, in turn, decrease the species preyed upon, and there is then a lack of food for the predators again; then some of them are eliminated, and the prey species have a chance to increase. So animals increase and decrease in numbers from year to year, sometimes as a result of apparent bad seasons and sometimes as a result of complex and obscure causes. A couple of arid seasons may be conducive to fires and cause a decrease in birds (Barnard 1927) but favor a high production of jackrabbits (Wooster 1935). When one species of rodent decreases, another often multiplies rapidly and to some degree takes its place (Middleton 1931, Pliater-Plokhotskii 1936). Specialized types are often less variable than generalized types—gulls are apt to vary more than terns in abundance because they depend on a wider range of ecological conditions (Tinbergen 1932). A species that has long occupied an area and attained a population equilibrium may combat more environmental resistance than one that is not established. The cecropia moths near Chicago are heavily infested with parasites but do not fluctuate greatly in numbers from year to year (March 1937).

Populations in Cultures.—In order better to understand the factors that influence populations there has lately been considerable study of small animals in cultures where conditions may be under control. Fruit flies have been reared on banana agar in milk bottles; protozoans have been carried along in culture media; and flour beetles have been maintained in standardized mixtures of cereals (Fig. 46). In such limited and uniform environments if one species is introduced it increases rapidly for a time, then more slowly, and finally remains nearly constant in numbers (Chapman 1931, Park 1933). If more than one species is present and one is predatory there may be various adjustments, and one or more may die out (Gause 1934). In flour, Park (1932) obtained more rapid increase when two pairs of flour beetles (Tribolium) were put into a culture medium than when one or more than two pairs were introduced. When the nutritive medium is of poor quality, populations increase slowly (L'Heritier 1934, Stanley 1934), but some organisms have more or less ability to change a medium so that it suits their

needs (Gause 1937). Crowding appears to be injurious generally, but Park (1933) observed more copulations and greater fertility in crowded flour-beetle cultures. Insects usually lay fewer eggs and increase more slowly in crowded cultures; also many eggs are eaten (Chapman & Whang 1934, Dustan 1935, Park 1933, Pearl 1932). In overpopulated cultures, growth of protozoans (Jahn 1929) and tadpoles (Lynn & Edelman 1936, Podhradsky 1931) is retarded; but the metabolism of fruit flies is more rapid (Scherbakov 1935). An environment is of course

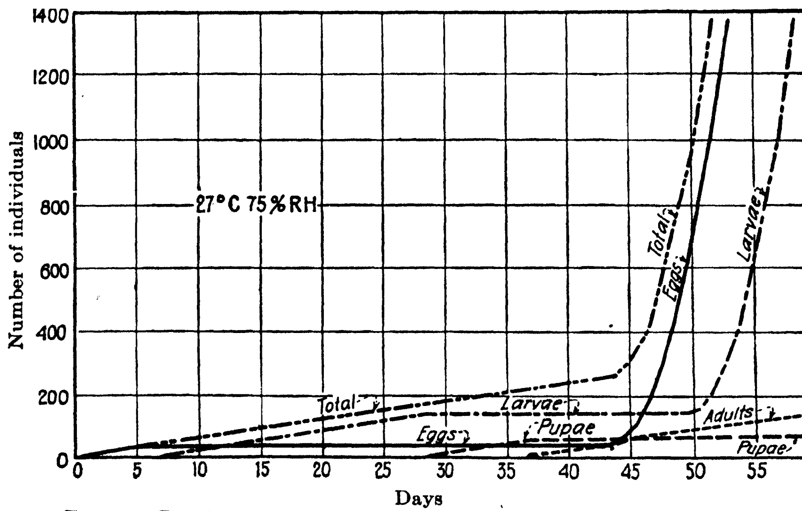


FIG. 46.—Population trends of *Tribolium confusum*, in standard flour cultures, from first oviposition of parent to oviposition of first progeny; at 27°C. and 75 per cent relative humidity. (*From Chapman* 1931.)

changed by crowding (Park 1937). In overpopulated aquariums infanticide among fishes has been observed to increase in direct relation to crowding, and a population suited to the volume of water available is thus maintained (Breder & Coates 1932). In cultures of Drosophila the ratios of expected hereditary classes may be changed by crowding, probably by differential mortality (Morgan & Tice 1914).

TERRITORY

Segregation.—As has been pointed out in Chapter V, species of animals tend to segregate into separate geographic areas and habitats. Even when two species occupy the same area, they

may not live in identical habitats or niches. A good example of this is furnished by two subspecies of salamanders which occur together through parts of Virginia, Maryland, and West Virginia. The selection of different habitats, in part at least due to differences in climbing abilities and avoiding reactions, enables *Desmognathus fuscus fuscus* and *D. f. carolinensis* to avoid competition (Noble & Evans 1932). Though these two types of salamanders occur in the same geographic areas, they really occupy separate territories, which are selected through the operation of distinctive and hereditary behavior patterns. Other instances of the same sort are given in Chapter V. These are different from those in which animals resort to particular areas, which serve them as homes and which they may defend against trespass with pugnacious tenacity.

Bird Territories.—Howard (1920) made a remarkable contribution to ecology in his "Territory in Bird Life" and stimulated study in that field. His book still remains a classic. Some birds defend particular areas which they apparently regard as their own homes and to which they return year after year. Certain species do this only during their breeding periods. Sea birds commonly resort to inaccessible cliffs or isolated islands, where they form great breeding colonies, but each bird selects its own particular area and guards it. Many birds while occupying an area sing continually to indicate to others of the same species that their home site is already reserved. On the arctic barrens where there is keen competition for desirable breeding areas many male birds arrive a couple of weeks before their mates. They sing to give notice that their home areas are occupied, fight tresspassers, and are continually on the alert to defend their territorial rights. Such rights are recognized by other birds of their own species. Sea birds on cliffs in the same latitude occupy very limited areas for nesting sites. Their food is in the sea and not adjacent to or directly connected with the nesting area. A male wren arrives at his summer home before his mate. He sings continually, fights, and even builds dummy nests to indicate that his territory is occupied. Even sea birds that live crowded together in immense colonies are jealous of the little space on which they actually nest (Dircksen 1932). Mockingbirds that live the year round in the same locality (Fig. 47) may defend home areas of different extent at different seasons

(Michner 1935). In most birds territory-defending behavior is apparent only during the breeding season, as Blanchard (1936) has shown for the white-crowned sparrow (Fig. 48). Some song sparrows remain on home areas at all seasons, males being more faithful in this than females; but others are present only during part of the year (Nice 1934).

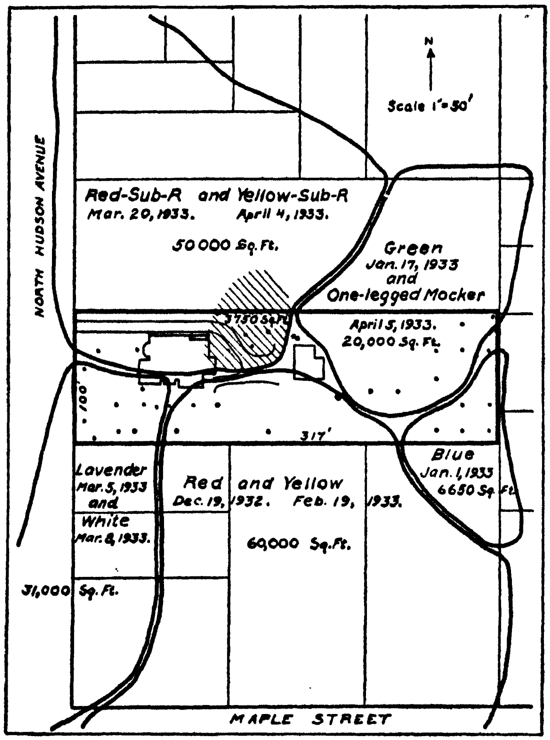


FIG. 47.—Map of mockingbird territories showing approximate areas occupied and dates on which territory holders were given colored bands, Pasadena, Calif. Shaded portion indicates winter territory of bird "yellow-sub-*R*" and later of "*AB-RG*." (*From Michner* 1935.)

Territories of Other Animals.—Many predaceous animals range over definite areas in search of food. The domestic dog and his wolf ancestor have very definite ideas of territorial rights. Lions hunt in packs of as many as 16 individuals of various ages and, though they change areas from time to time, cover rather definite territories. The herds of grazing ungulates in Africa, such as the springbuck, wildebeest, hartebeest, and gazelle,

remain on definite areas in their wanderings. Heape (1931) summarizes certain observations of Seton in Canada and gives the average territorial ranges of several mammals as follows: white-tailed deer, 200–300 acres; moose, 30 sq. miles; bison, 60,000 sq. miles; beaver, 0.5 sq. mile; porcupine, 1 sq. mile; weasel, 10 sq. miles; black bear, 125 sq. miles, grizzly bear, 625 sq. miles. A red squirrel claims two or three trees as his home and will fight intruders who invade this area. Another

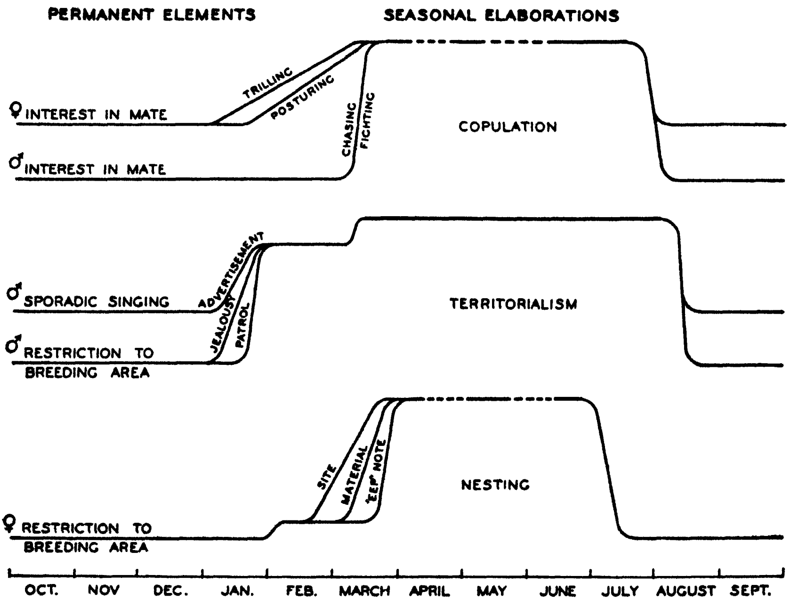


FIG. 48.—Relation of permanent and seasonal elements of behavior of white-crowned sparrow, Berkeley, Calif. (*After Blanchard* 1936.)

squirrel may have a similar home some distance away. The two individuals hunt over intermediate areas with impunity and even play together; but if one enters the territory of the other, he is attacked. Howling monkeys travel about through tree-tops over definite areas, and bands have great respect for the territorial rights of others (Carpenter 1934). Some lizards defend areas on the ground or in trees. Certain male fishes are extremely resentful of any invasion of their nesting areas. Various spiders, insects, and crabs defend their territorial rights. A fiddler crab is quick to fight another that encroaches on the mud about the mouth of his burrow.

Reasons for Territorialism.—Usually animals that look upon particular areas as their homes and private property are led to do so by limited food supplies or an urge to make conditions safe for their offspring. Plovers defend areas that are of considerable size, large enough to provide food for their brood of young. A wandering carnivore has a certain recognized area over which he hunts for prey. Thus he avoids controversies with others of his kind and through most of his year can devote his efforts to hunting, not fighting. A male bass clears off a bed of pebbles on the bottom of a pond and there induces a female to lay eggs. He then watches the eggs with jealous care, attacking intruders and fanning his prospective offspring with his fins in order to remove dirt and keep the water aerated. An animal that confines its activities to a limited area becomes so familiar with its surroundings that it saves much time and trouble. It learns where food is most likely to be found, where enemies may lurk, where there are refugees, and other useful information. Thus it lives in greater safety and with more assurance of finding food.

CLASSIFICATION OF COMMUNITIES

In the following summary of communities into which animals may be grouped the terminology of Clements (1936) has been used. Groupings are about the same as those presented in the first edition of this work. Certain of the writer's groups have been criticised (Hora 1930, etc.), but on the whole so little progress has been made in the analysis of communities during the past 12 years that the scheme is left essentially unchanged, and suggestions for revisions are discussed in appropriate places in the next three chapters.

Synopsis of Communities

SUPERREALM α. AQUATIC.

- **REALM I. MARINE.**
  - **PROVINCE A.** Littoral.
    - **Formation 1.** Hard beaches.
      - ASSOCIATION *a*. Rock walls.
        - **Fasciation 1.** Zone above high tide.
        - **Fasciation 2.** Intertidal zone.
        - **Fasciation 3.** Laminarian zone
        - **Fasciation 4.** Shorewater.

Association *b.* Pebbly beaches.
Fasciation 1. Zone above high tide.
Fasciation 2. Intertidal zone.
Fasciation 3. Laminarian zone.
Fasciation 4. Shorewater.
Association *c.* Piles, wharves, and ships.
Fasciation 1. Surface.
Fasciation 2. Boring.
Formation 2. Shifting beaches.
Association *a.* Clay beaches.
Fasciation 1. Drift line.
Fasciation 2. Intertidal zone.
Fasciation 3. Below low tide.
Fasciation 4. Shorewater.
Association *b.* Sand beaches.
Fasciation 1. Drift line.
Fasciation 2. Intertidal zone.
Fasciation 3. Below low tide.
Fasciation 4. Shorewater.
Association *c.* Mud beaches.
Fasciation 1. Drift line.
Fasciation 2. Intertidal, exposed mud flats.
Fasciation 3. Among or under plants.
Fasciation 4. Lagoons.
Fasciation 5. Shorewater.
Association *d.* Estuaries and sounds.
Fasciation 1. Freshwater.
Fasciation 2. Brackish water.
Fasciation 3. Marine.
Association *e.* Marshes.
Fasciation 1. Freshwater.
Fasciation 2. Brackish water.
Fasciation 3. Marine.
Province B. Open ocean, pelagic.
Formation 1. Shorewater.
Association *a.* Above depths of 150 m.
Fasciation 1. Plankton.
Fasciation 2. Nekton.
Association *b.* Between depths of 150 and 500 m.
Fasciation 1. Plankton.
Fasciation 2. Nekton.
Formation 2. Oceanic.
Association *a.* Pelagic, above depths of 150 m.
Fasciation 1. Plankton.
Fasciation 2. Nekton.
Association *b.* Between depths of 150 and 1,500 m.
Fasciation 1. Plankton.
Fasciation 2. Nekton.

ASSOCIATION *c*. Pelagic, below depths of 1,500 m.
Fasciation 1. Plankton.
Fasciation 2. Nekton.
PROVINCE C. Bottom.
Formation 1. On continental shelves.
ASSOCIATION *a*. Terrigenous deposits.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
ASSOCIATION *b*. Calcareous oozes.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
Formation 2. Abyssal bottom.
ASSOCIATION *a*. Calcareous oozes.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
ASSOCIATION *b*. Siliceous oozes.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
ASSOCIATION *c*. Red clay.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
REALM II. FRESHWATER.
PROVINCE A. Flowing water (lotic).
Formation 1. Rapidly flowing streams.
ASSOCIATION *a*. Springs.
Fasciation 1. Surface of water.
Fasciation 2. Surface of bottom.
Fasciation 3. Attached to bottom.
Fasciation 4. Attached plants.
Fasciation 5. Pools.
Fasciation 6. Below surface of bottom.
ASSOCIATION *b*. Brooks.
Fasciation 1. Surface.
Fasication 2. Nekton.
Fasciation 3. Plankton.
Fasciation 4. On bottom, attached.
Fasciation 5. Plants.
Fasciation 6. Pools.
Fasciation 7. Below surface of bottom.
Formation 2. Slowly flowing streams.
ASSOCIATION *a*. Creeks.
Fasciation 1. Surface.
Fasciation 2. Nekton.
Fasciation 3. Plankton.
Fasciation 4. Attached vegetation.
Fasciation 5. Bottom.
ASSOCIATION *b*. Rivers.
Fasciation 1. Bottom lands.

Fasciation 2. Shore.
Fasciation 3. Surface.
Fasciation 4. Plankton.
Fasciation 5. Nekton.
Fasciation 6. Bottom.

PROVINCE B. Standing water (lentic).

SUBPROVINCE B(a). Lacustrine.

Formation 1. Littoral.

ASSOCIATION *a*. Hard beaches.
Fasciation 1. Beach above water.
Fasciation 2. Shore line.
Fasciation 3. Rachion.
Fasciation 4. Attached vegetation.
Fasciation 5. Sublittoral zone.
Fasciation 6. Shorewater.

ASSOCIATION *b*. Sandy beaches.
Fasciation 1. Beach above water.
Fasciation 2. Shore line.
Fasciation 3. Rachion.
Fasciation 4. Submerged beach below rachion.
Fasciation 5. Sublittoral zone.
Fasciation 6. Shorewater.

ASSOCIATION *c*. Muddy beaches.
Fasciation 1. Beach above water.
Fasciation 2. Surface of water.
Fasciation 3. Shore line.
Fasciation 4. Rachion.
Fasciation 5. Vegetation zone.
Fasciation 6. Sublittoral zone.
Fasciation 7. Shorewater.

ASSOCIATION *d*. Lagoons.
Fasciation 1. Beach above water.
Fasciation 2. Surface of water.
Fasciation 3. Shore line.
Fasciation 4. Rachion.
Fasciation 5. Vegetation.
Fasciation 6. Shorewater.

ASSOCIATION *e*. Estuaries.
Fasciation 1. Plankton.
Fasciation 2. Vegetation.
Fasciation 3. Bottom.
Fasciation 4. Littoral.

Formation 2. Limnetic.

ASSOCIATION *a*. Epilimnion.
Fasciation 1. Plankton.
Fasciation 2. Nekton.

ASSOCIATION *b*. Hypolimnion.
Fasciation 1. Plankton.
Fasciation 2. Nekton.
Formation 3. Bottom in deep water.
ASSOCIATION *a*. Bottom of moderately deep lakes having variable bottom temperatures.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
ASSOCIATION *b*. Bottoms of deep lakes having cool bottom temperatures.
Fasciation 1. Below or on surface of bottom.
Fasciation 2. Above bottom.
SUBPROVINCE B(b). Ponds.
Formation 1. Littoral.
ASSOCIATION *a*. Ponds with bare bottoms.
Fasciation 1. Beach above water.
Fasciation 2. Surface.
Fasciation 3. Shore line.
Fasciation 4. Shorewater.
Fasciation 5. Bottom.
ASSOCIATION *b*. Ponds containing vegetation.
Fasciation 1. Beach above water.
Fasciation 2. Surface.
Fasciation 3. Shore line.
Fasciation 4. Vegetation.
Fasciation 5. Shorewater.
Fasciation 6. Bottom.
SUBPROVINCE B(c). Swamps and pools.
Formation 1. Swamp and bog organisms.
ASSOCIATION *a*. Swamps.
Fasciation 1. Vegetation above water.
Fasciation 2. Surface.
Fasciation 3. Submerged vegetation.
Fasciation 4. Swamp water.
Fasciation 5. Bottom.
ASSOCIATION *b*. Bogs.
Fasciation 1. Vegetation above water.
Fasciation 2. Surface vegetation.
Fasciation 3. Surface.
Fasciation 4. Water.
Formation 2. Pools.
ASSOCIATION *a*. Pools with hard bottoms.
Fasciation 1. Surface.
Fasciation 2. Water.
Fasciation 3. Bottom.
ASSOCIATION *b*. Pools with muddy bottoms.
Fasciation 1. Surface.
Fasciation 2. Water.
Fasciation 3. Bottom.

PROVINCE C. Flowing water in caves.
Formation 1. Rapidly flowing streams.
ASSOCIATION *a*. Springs and brooks.
Fasciation 1. Flowing water.
Fasciation 2. Bottom.
Formation 2. Slowly flowing streams.
ASSOCIATION *a*. Creeks and rivers.
Fasciation 1. Flowing water.
Fasciation 2. Bottom.
PROVINCE D. Standing water in caves.
Formation 1. Lakes and pools.
ASSOCIATION *a*. Littoral.
Fasciation 1. Open water.
Fasciation 2. Bottom.
PROVINCE E. Ground waters.
Formation 1. Ground waters.
ASSOCIATION *a*. Ground waters.
Fasciation 1. In soil.
Fasciation 2. Crevices.

SUPERREALM β. TERRESTRIAL.

REALM I. TERRESTRIAL.
PROVINCE A. Subterranean.
Formation 1. Soil.
ASSOCIATION *a*. Clay soils.
Fasciation 1. Visiting surface.
Fasciation 2. Not visiting surface.
ASSOCIATION *b*. Humus.
Fasciation 1. Visiting surface.
Fasciation 2. Not visiting surface.
ASSOCIATION *c*. Sandy soils.
Fasciation 1. Visiting surface.
Fasciation 2. Not visiting surface.
ASSOCIATION *d*. Rocks.
Fasciation 1. On surface.
Fasciation 2. Crevices.
Formation 2. Cave.
ASSOCIATION *a*. Transient.
Fasciation 1. Moving on solid or liquid substrata.
Fasciation 2. Flying.
ASSOCIATION *b*. Permanent residents in caves.
Fasciation 1. Moving on solid or liquid substrata.
Fasciation 2. Flying.
PROVINCE B. Above surface of soil.
Formation 1. Surface.
ASSOCIATION *a*. Wet ground.
Fasciation 1. Subterranean.
Fasciation 2. Surface.
Fasciation 3. Above the surface.

ASSOCIATION *b*. Medium-dry ground.
Fasciation 1. Subterranean.
Fasciation 2. Surface.
Fasciation 3. Above the surface.
ASSOCIATION *c*. Dry sand.
Fasciation 1. Subterranean.
Fasciation 2. Surface.
Fasciation 3. Above the surface.
ASSOCIATION *d*. Rock.
Fasciation 1. Crevice.
Fasciation 2. Surface.
Fasciation 3. Above the surface.

Formation 2. Associated with terrestrial plants.
ASSOCIATION *a*. Forests.
CONSOCIATION *a*(1). Coniferous forests.
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Trunks and branches.
Fasciation 3. In wood.
CONSOCIATION *a*(2). Deciduous dicotyledonous forests.
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Trunks and branches.
Fasciation 3. In wood.
CONSOCIATION *a*(3). Evergreen dicotyledonous forests.
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Trunks and branches.
Fasciation 3. In wood.
ASSOCIATION *b*. Shrubs.
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Trunks and branches.
Fasciation 3. In wood.
ASSOCIATION *c*. Low plants (1 to 6 ft.).
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Within plants.
ASSOCIATION *d*. Desert.
Fasciation 1. Leaves, twigs, and fruits.
Fasciation 2. Within plants.

Formation 3. Aerial.
ASSOCIATION *a*. Ballooning and gliding.
Fasciation 1. Ballooning.
Fasciation 2. Gliding.
ASSOCIATION *b*. Flying.
Fasciation 1. Associated with water or vegetation.
Fasciation 2. Habitually flying in the air.

APPENDIX I. Islands.
APPENDIX II. Structures made by man.

SUPERREALM Γ. CONSORTIC.

CHAPTER VIII

THE OCEAN

The ocean constitutes 72 per cent of the surface of the earth. It has apparently contained animals longer than freshwater or

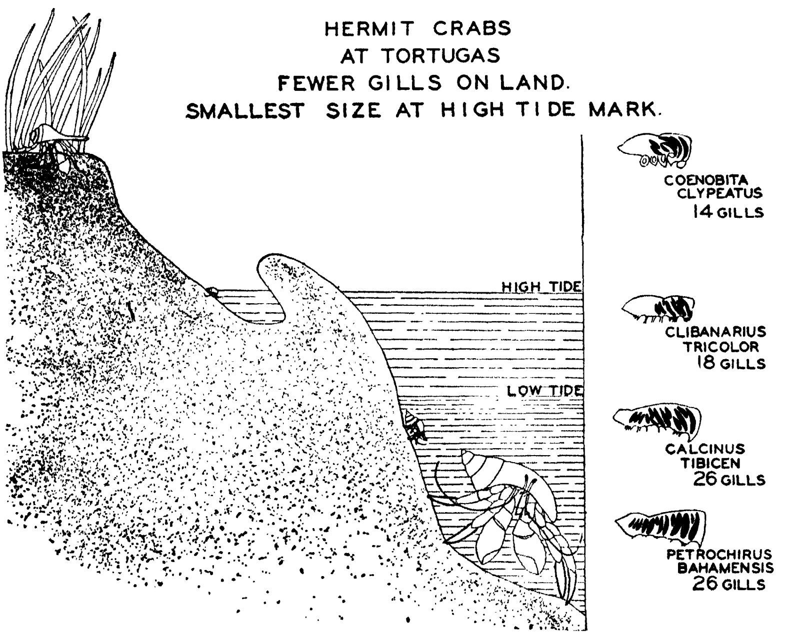


Fig. 49.—Adaptations of four species of hermit crabs. (*From Pearse* 1936.)

land habitats. The antiquity of the ocean is indicated by the fact that the fossils from the earliest known geological ages are all marine. At present the distribution of a considerable number of great groups of animals is limited to the ocean (Ctenophora, Brachiopoda, Echinodermata, Polychaeta, Cephalopoda, Tunicata). All types of animals that are found in land and freshwater habitats are also found to some extent in the ocean, except the Myriapoda and Onychophora. The sponges, coelenterates,

and bryozoans, though represented by many species in the ocean, are few in freshwater. Such facts have led to the rather general belief that life originated in the ocean and later invaded freshwater and land habitats. Some groups of animals are at the present time progressing toward land and show characteristic adaptations. For example, crustaceans (Figs. 49, 50) show reduction in gills and blood salinity as they go toward land

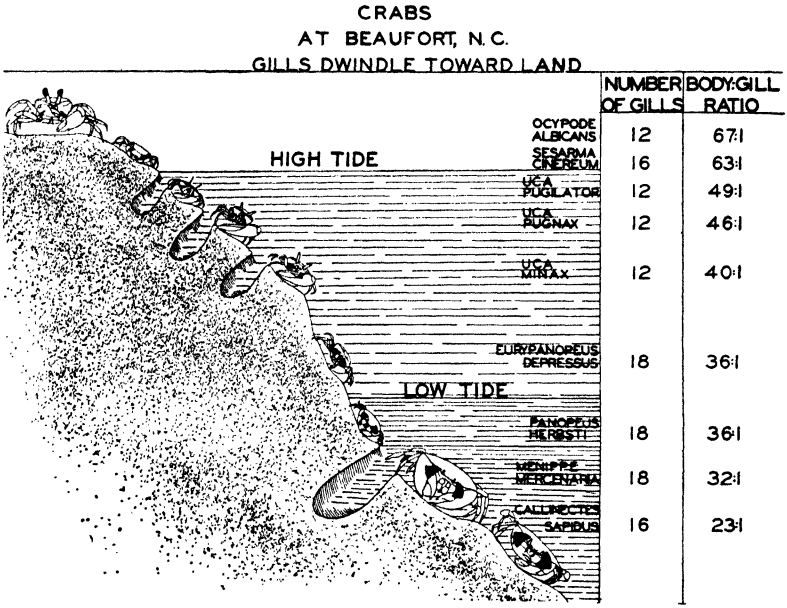


FIG. 50.—Reduction of gill numbers and volumes in crabs toward land. (*From Pearse* 1936.)

(Pearse 1929, 1932, 1936). The land hermit crab, *Coenobita clypeatus* (Herbst), can live for three months in air after its gills have been removed. Many speculative evolutionists have believed, and still believe, that life came into being along the seashore; but Heilprin (1887) and Brooks (1893–1894) advocated the view that life first appeared in the open ocean. Most marine animals are poikilothermal, and those that are homoiothermal have apparently, judging from paleontological evidence, been derived rather recently from freshwater or land habitats. Some animals, such as insects (Buxton 1926) and mites, adapted primarily to terrestrial life, have secondarily taken up life in the

ocean, probably to take advantage of the food resources and general stability that obtains there. Marine insects are not all primitive but include collembolans, bugs, odonates, caddisflies, beetles, and dipterans. Diptera appear to be able to endure higher salinities than other insects (Thorpe 1931), in some cases much above that of the ocean. Marine vertebrates are often able to invade nonoceanic waters of high salinity if such waters contain calcium (Pearse 1936), but the invasion of saline waters by insects is apparently not concerned with that element (Thorpe 1932). The ocean has long constituted a rather uniform, favorable dwelling place for animal life. Because the animals near the poles of the earth show greater similarity to each other than to those in intervening tropical and temperate regions, several writers (Murray 1898, Pfeffer 1901, and Pratt 1901) have supported a theory of "bipolarity." These men postulate an ocean of rather uniform temperature from pole to pole during Tertiary times and a corresponding uniform distribution of animal life. The remnants of the Tertiary fauna are believed to persist today near the poles but have changed or been displaced by other animals toward the equator.

The Ocean as a Habitat.—As a dwelling place for animals the ocean offers unusual stability in temperature, salinity, and gaseous content. The general chemical and physical conditions of life vary slowly and to a lesser degree than in freshwater and on land. These are discussed in detail in such books as those of Harvey (1928) and Marmer (1930).

Salinity.—The average salinity of the ocean is about 3.5 per cent (Fig. 51). Freshwater seldom has a salinity of 1 per cent, and its fauna, according to Hirsch (1915), is usually not able to tolerate a salinity greater than 2–3 per cent. In the past, calcium and potassium probably have been decreasing, and sodium and magnesium have been increasing in sea water. Johnstone (1908) suggests that vertebrates and certain other animals use such a large percentage of lime in building their skeletons because they established their metabolic habits long ago when the ocean was rich in calcium. Many marine animals (corals, etc.) can survive a 20 per cent decrease in salinity, and Vaughan (1919) interprets this as evidence that the ocean is growing more salty. Flattely and Walton (1922) state that the primordial ocean contained no salts or nitrogen that was available

for living things but that the modern ocean is an "ideal medium for life." Lime-secreting organisms are more active at present in warm oceans, and their presence in Tertiary deposits led Pfeffer (1901) to conclude that the Tertiary ocean had a higher and more uniform temperature than now. The salts in sea water are mostly chlorides and sulphates, with smaller (but for certain

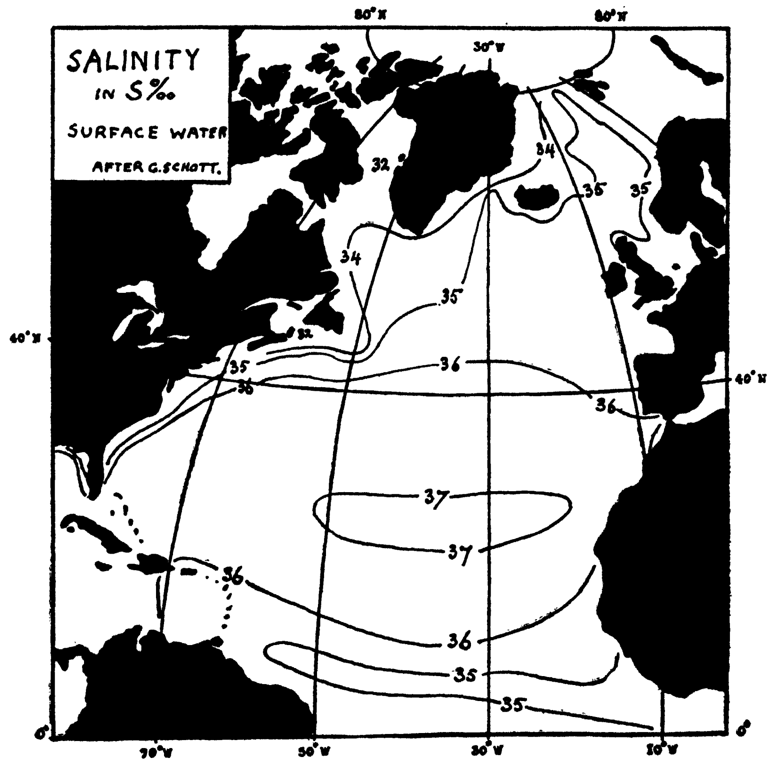


FIG. 51.—Salinities in North Atlantic Ocean in grams per liter. (*After Harvey* 1928.)

animals no less important) quantities of bromides, carbonates, and other compounds. At least 24 metals are present, but those in largest quantity are sodium, magnesium, calcium, and potassium. Small amounts of copper and zinc are found in many marine animals. The ratio between the different salts in the ocean remains rather constant with variations in salinity, except that the amount of calcium increases with depth. Murray

(1914) gives averages for the salts in sea water in parts per thousand:

Sodium chloride	27.213
Magnesium chloride	3.807
Magnesium sulphate	1.658
Calcium sulphate	1.260
Potassium sulphate	0.863
Calcium carbonate	0.123
Magnesium bromide	0.076
Total	35.000

Oxygen and carbon dioxide vary in amount. Except in rare cases, such as the deeper water of the Black Sea, there is enough oxygen at all depths to supply the needs of plants and animals (Grote 1934). Oxygen, on account of its solubility in sea water, has a higher ratio to nitrogen in the ocean (34:66) than in the atmosphere (21:79). Atkins (1923, 1923*a*, 1923*b*, 1923*c*) has recently studied the dissolved chemicals in the sea near Plymouth. He found that there were seasonal variations in alkalinity; that algae rapidly used up phosphates and that the water contained little of free phosphates from May to August; that diatoms required and used silica; and that traces of oxidizable organic matter were present. On the New England coast Rakestraw (1932) found that phosphate and nitrate increased offshore toward the edge of the continental shelf. In the same locality the remains of plants have been found to form a jelly-like substance which moves about in currents and carries sand grains and other objects (Raymond & Stetson 1931). Vaughan (1919) has demonstrated that the precipitation of lime to form coral reefs is due to bacteria more than to corals. On the coast of Japan there are six species of oysters, each of which has its particular range of salinity toleration (Amemiya 1928). Danois (1924) showed that the movements of the haddock were influenced by salinity, the fishes ranging where the variation was between 35.4 and 35.5 parts per thousand. He divides the ocean into four general regions according to temperature and salinity: Arctic, −1°C., 35–35.5 parts; Abyssal, +4°C., 35 parts; Continental, temperature variable, 33–34 parts; Equatorial, warm, 35+ parts.

Depth in Relation to Marine Life.—Life occurs at all depths in the ocean (Murray 1898), but the photic zone, where the manu-

facture of living substance through photosynthetic activity is possible, extends down to only about 3,000 ft. and the number of species and individuals decreases steadily at greater depths. Only 5 per cent of the ocean has a depth of over 3,000 fathoms. Pressure increases about 1 atmosphere for each 33 ft., so that abyssal animals are subjected to enormous pressures. Water is not absolutely incompressible, and it has been estimated that, if gravity should cease, the ocean level would rise about 200 ft. Murray (1914) gives pressure above that of the atmosphere at various depths as follows: 33 ft., 15 lb.; 99 ft., 45 lb., 100 fathoms, 270 lb.; 1,000 fathoms, 1.2 tons; 5,000 fathoms, 6 tons per square inch.

Light in Relation to Marine Life.—The living plants in the ocean are, of course, dependent on light and hence are confined to the upper 3,000 ft. Most of them are algae, but Zostera is often abundant along shores, and a few other phaenerogams occur. Light and plant life occur at greater depths in tropical waters than elsewhere. Huntsman (1920) says: "The depths of the sea experience a never-ending, starless night and the intermediate waters enjoy a brief daily bluish twilight." Shelford and Gail (1922) working near Seattle found that in calm, clear weather 25 per cent of sunlight was cut off by the surface of the ocean; in rough weather such loss reached 60 to 70 per cent. The penetration of light is, of course, limited not only by roughness of the surface but also by turbidity. Along the shore a zone of brown algae usually occurs at depths between 5 and 20 m., where shorter wave lengths are about 10 per cent of those of total sunlight and where red wave lengths are about 99 per cent. Red algae usually occur between 10 and 30 m. They begin where red and orange light is reduced to about 1 per cent of daylight and extend to where it is approximately 0.0032 per cent. Barnacles (*Balanus balanoides*) grow best in the intertidal zone where there is least illumination (Klugh & Newcombe 1935).

Temperature in Relation to Marine Life.—The minimum temperatures of the ocean vary in polar seas from −2.22 to 16.7°C., and the maximum of those of the tropics from 26.67 to 32°C., yet the ocean shows less variation than the atmosphere, which ranges from −45 to 50°C. The ocean absorbs and loses heat only one-fourth as rapidly as land, hence has greater thermal stability. Below depths of 600 ft. there is little or no seasonal

variation in temperature, the mean being about 2.5°C. Cold sea water will always sink through warmer water of equal salinity. Dense water, produced at the surface by evaporation, may sink and warm deeper strata. Temperature is the primary cause of the vertical and horizontal zonation that animals show in their distribution. Huntsman (1920) makes 12 climatic zones in the North Atlantic and in another paper (1918) shows that the fishes and other animals in the Gulf of St. Lawrence are arranged in vertical strata according to temperature. Setchell (1922) questions the value of such terms as eurythermal and stenothermal as indicative of the actual range of marine plants. He studied 34 species of marine algae and found that 26 were stenothermal in zones having an amplitude of 5°C.; 6 were somewhat eurythermal; and 2 were broadly eurythermal (15°C. range). He points out that plants may have a wider range than their ability to reproduce would indicate. For example, *Zostera marina* grows well between 10 and 20°C. but usually reproduces only between 15 and 20°C. Stenothermal plants are said to be particularly characteristic of the tropics (Setchell, 1920), and in all seas plant zonation is believed to be closely related to temperature. Danois (1924) has shown that the cod frequents cold water (−2 to +6°C.). In warmer seasons it deserts the banks, and fishing is accordingly poor. The herring is known to swim at greater depths in summer. Orton (1920) affirms that temperature largely controls distribution and reproduction of life in the ocean and points out that breeding usually starts at the beginning of periods of maximum or of minimum temperatures and continues as long as conditions are favorable.

Tides and Currents.—Tides and currents (Figs. 18, 19), especially in shallow water, exercise important influences on the ocean, particularly in regard to temperature. The two primary causes of oceanic circulations are winds and differences in pressure due to variations in water level. Land barriers, friction, and the earth's rotation also influence water movements. Off the coast of New England the great eddies "correspond to the conformation of the deeper basins rather than to the shore line and are to be ascribed to the action of the rotation of the earth on the tidal oscillations and the oscillations resulting from barometric gradients" (Huntsman 1923*a*). Flattely (1921) has suggested that the ebb and flow of the tides have led to the

development of terrestrial habits in certain types of animals through rhythmical exposure to air and desiccation. Animals living in the intertidal zone must also have considerable resistance

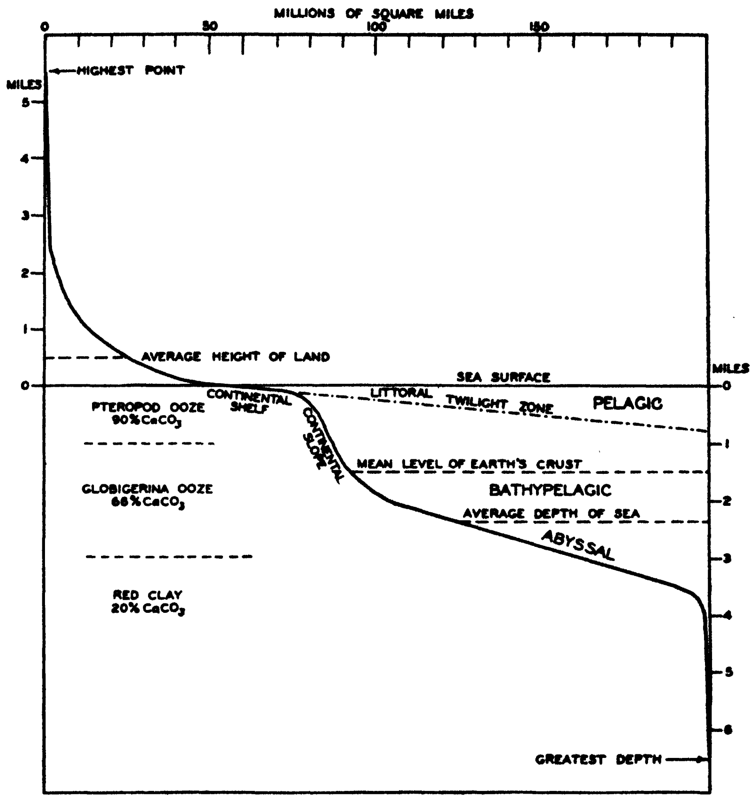


FIG. 52.—Regions, depths, and bottom deposits in ocean and altitudes on land.

to rapid thermal variations. Huntsman (1918*b*), in speaking of the fishes along the Canadian coast, says:

> Our major conclusions are that the absence of heavy tides makes the Gulf of St. Lawrence, and in particular the Magdalen shallows, an important spawning ground for many species of fishes with pelagic eggs, and the presence of heavy tides prevents the Bay of Fundy serving in a similar capacity, excludes from it the mackerel, and is of prime importance in the fishery for young herring or sardines.

Movements in ocean water are much more limited in rate and extent than those in the atmosphere, but the great currents have

important influences on climate and serve to distribute animals and transport food. "The popular conception of 'rivers in the ocean' should be replaced by one of eddies or swirls varying about the prevailing current systems" (McEwen 1919). Seasonal succession and general marine stabilization are often related to vertical circulations. Many currents show cyclical variations, often correlated with seasonal changes.

Strata in the Ocean.—The stratification, or zonation, of marine habitats is striking (Fig. 52). Such arrangement of animals in appropriate habitats is due primarily to variations in temperature, light, and bottom. A photic zone extends down to nearly 3,000 ft. Below that is the aphotic ocean. The temperature near the surface is comparatively warm and variable; that at great depths is constant, and the water is nearly immobile. Near land, the ocean bottom may consist of various types of deposits. In deeper water there is a uniform substratum of ooze, lime shells extending down to a depth of 2 miles and being succeeded at great depths by fine red clay. Pfeffer (1901) divided the ocean into three regions:

1. Surface—light, plants, currents, often a warm surface stratum down to 50 to 150 fathoms.
2. Subsurface—cool, homothermal, no light or plants, food from above, 600 to 1000 fathoms.
3. Deep sea—no light, no temperature variations, no plants, food from pelagic region, bottom of ooze or clay.

Murray (1898) distinguished seven regions:

1. Littoral and Shallow Water—littoral down to 20 fathoms; sublittoral 20 to 100 fathoms.
2. Surface Oceanic Fauna and Flora.
3. Mud-line Fauna—just below 100 fathoms.
4. Intermediate, or Twilight, Fauna of Open Sea.
5. Archibenthal Fauna of Continental Slope—100 to 1700 fathoms.
6. Deepwater Intermediate Fauna—below 1700 fathoms.
7. Abyssal Benthoic Fauna—below 1700 fathoms.

Flattely and Walton (1922) make four divisions of the ocean: (1) Strand or Tidal Zone, (2) Shallow Sea, (3) Pelagic, (4) Abyssal. They also differentiate the marine plant zones as

1. Free or floating plant—plankton.
2. Fixed plants—benthos:
   a. Littoral—to low-water mark.
   b. Sublittoral—to lowest limits of seaweeds.
   c. Elittoral—no vegetation.

These diverse classifications make it apparent that there has been no uniformity of usage in regard to the regions in the ocean.

Marine Food Resources.—The sea is a great conservator. It receives, digests, and stores much matter that has been swept from the land and that has been produced by the activities and disintegrations of aquatic organisms. Brooks (1893) stressed the fact that the great food resources of the ocean were in the plants of the pelagic region. He said:

> We may regard the great primary food supply as made up of two simple protozoa, Globigerina and the radiolarians, and some five or six unicellular plants.

He also pointed out that the pelagic food resources must be very old because such a large part of the ocean fauna is adjusted to and dependent upon them. Brant (1901) likewise dwelt upon the importance of plants as the source of marine food and pointed out that nitrogen compounds were not abundant in sea water, probably because they were broken up by denitrifying bacteria. He noted that there were relatively more of nitrogenous compounds in cold seas because there were fewer putrefying bacteria there. He also believed that both nitrifying and denitrifying bacteria were present in the ocean, but Lipman (1922) has recently produced evidence that the former are absent from or cannot function in sea water. If Lipman is right, it follows that marine organisms are dependent to a considerable degree on land and freshwater habitats for their nitrogenous compounds. This is what Johnstone (1908) and others have long maintained. Osborn (1917) takes the position that life could not have originated in the ocean because enough available nitrogen was not present. From studies on stored sea water Keys, Christensen, and Krogh (1935) conclude that bacteria may liberate some ammonia from sea water which is free from colloids and particulate matter. Herdman (1907) believed that available calcium and nitrogen were essential and limiting factors in the development of life in the ocean and that these compounds are continually

taken into and excreted by marine organisms; but Atkins (1930) has recently shown that calcium is never a limiting factor, phosphorus usually is, and nitrogen may be. On the last cruise of the *Carnegie* a positive correlation was found in the Pacific between phosphate content of the upper water layers and quantity of phytoplankton. A study of other correlations and subsurface conditions indicated that the differential distribution of plankton in the open Pacific is caused largely by differences in the vertical circulation in the upper few hundred meters. This circulation is probably the chief factor in renewal of nutrient salts in the photosynthetic zone (Graham 1934). Ritter (1918) has shown that the Pacific has less of Sargassum and Globigernia than the Atlantic and is, in general, more barren. Life in the ocean, on the whole, grows more abundant toward the surface, and animals living below are always dependent directly on the organic material that is manufactured there, largely through the use of solar energy.

The Ocean as a Favorable Environment.—Animals living in sea water are continually surrounded by a medium that is quite similar to their own body fluids. The blood of many marine invertebrates is like sea water in its salt content and osmotic pressure. The blood of marine vertebrates resembles sea water less closely but still shows a general similarity to it. In many respects the ocean is perhaps the most favorable realm in which animals live. It is relatively constant in temperature and in oxygen and carbon dioxide content. In the open sea in all parts of the world Miller (1934) found pH varying between 7.83 and 8.23, whereas temperatures ranged from 11.0–29°C. The sea is a solution of the chemicals from which protoplasm is readily built up.

PROVINCE A. LITTORAL REGIONS

The littoral region may be defined as that area of coastal waters that comes within the oscillation of waves, however induced (Ercegovic 1934). Perhaps the most important factor on marine beaches is the tidal rhythm, and littoral animals show more or less adjustment to it. Animals living in the intertidal zone lead a hard life. They are subject to the impact of waves and endure alternating periods of wetting and desiccation, which are often associated with striking changes in temperature. When the tide flows, it brings food, and with its advent barnacles,

mussels, and other shore animals begin to feed on the myriads of microscopic organisms that are swept in from the open sea. The rising tide also gives a band of voracious predators an opportunity to migrate up the beach and devour helpless shore animals. Fishes, crustaceans, snails, starfishes, and others periodically come inshore to seek food. Probably on this account such animals as mites (King 1914), fiddler crabs (Pearse 1913), and podurans (Davenport 1903*a*) remain inactive or safely enclosed in burrows while they are covered with water. On the other hand, such animals, as Renilla (Parker 1920), Actinia (Crozier 1921*c*), worms, Lingula, and clams contract when exposed to the air and expand when they are immersed. Some animals find refuges in pools at low tide or hide under vegetation. When the tide ebbs, a resident and foreign army seeks food in the intertidal zone. Gulls, crows, rats, sandpipers, crabs—even lizards and frogs—come to forage. The drift line is picked over by crabs, amphipods, beetles, and other scavengers.

Fecundity and Growth of Littoral Animals.—The animals on ocean beaches have many opportunities to die and usually have great propagative powers. Field (1922) observed a mussel that laid 12,000,000 eggs in a quarter of an hour. He found that mussels grew more rapidly if they chanced to rest in sheltered situations, where they had opportunity to feed from tidal water and were also protected from some of the vicissitudes of littoral life.

Coloration of Littoral Animals.—Among shore animals protective coloration is often developed to a striking degree, and many species have variable patterns which closely resemble the backgrounds on which they rest (Keeble & Gamble 1904). Some, like the flounder (Mast 1916), are able to change their colors and patterns to match changing backgrounds. Decorator crabs cover their backs with bits of seaweed and other objects so that they resemble their surroundings closely (Pearse 1911).

Littoral Temperatures.—Temperatures in littoral habitats are variable. An animal attached to a rock may be baked in the rays of a summer sun and the next moment deluged with cool water. Many littoral animals are able to endure wide and sudden variations in temperature, and stenothermic species are usually found in habitats where there is little change. Experiments by the U. S. Bureau of Fisheries show that lobster fry

will not develop in water below 11°C., though adults will live and eggs hatch at lower temperatures. The Pismo clams of the west coast of North America live above low-tide mark during the first three years of their lives. A case has been described (Ecology 4:45) in which these clams during a cold wave were numbed to such an extent that they could not burrow. They were then washed out of the sand by the waves and devoured in great numbers by gulls and pelicans. Shelford (1916) tested resistance to high temperatures as shown by crustaceans of the same species from deep and from shallow water. He found that those from deep water (100 m.) died more quickly. In polar seas the temperature is never warm, and often there is little distinction between littoral faunas and those below. The upwelling of the Humbolt Current along the western coast of South America permits antarctic animals to range farther north than they would otherwise be able to (Murphy 1923). Temperature is an important factor in limiting the local and geographic range of many littoral animals.

Littoral Vegetation.—Shore vegetation is distinctive and differs from that of the open sea in being larger and attached. Cowles (1902) states that plants growing above freshwater and ocean beaches are strikingly alike. There are the following strata: (1) a barren zone just above the water; (2) pioneer plants, such as sea rocket, sea spurge, and beach pea; and (3) a higher zone where sand reeds and other plants are characteristic. Warming (1909) points out that submerged marine plants that grow on loose bottoms are ribbon-like and become narrow in shallow water. Martin (1922) states that eelgrass is the most important plant on soft bottoms, that the brown algae (Fucus, Ascophyllum, etc.) characteristically cover exposed rock surfaces, and that Ulva and Enteromorpha typically occur on "flats" in rather quiet water. Red algae are commonly found below low-tide mark, and many of them form calcareous coverings over their own surfaces. There are more bacteria in littoral waters than in the open sea (Johnstone 1908). Shore diatoms have resting spores, and those in the pelagic province do not. The attached shore vegetation is a source of food for many animals but sometimes does injury by overgrowing and smothering such animals as mussels (Field 1922) and barnacles. Many annual littoral algae are found only at certain seasons (Bell 1927). Allee (1923*a*)

found that there was usually more oxygen over beds of attached vegetation than elsewhere.

Littoral Zonation.—Though there are numerous transitional areas, littoral animal formations and associations are rather clearly defined according to the character of the bottom. Allee (1934) separates marine littoral habitats into two groups, those of eroding and those of depositing shores. Animals of hard bottoms (rock, piles, and to some extent clay) are, as a rule, quite distinct from those on shifting bottoms (sand, mud), but the propagative phases of the former are so abundant in shore water that they usually occupy every firm surface, however small or isolated from other suitable areas. Allee (1923) found that mud flats constituted a remarkably independent habitat, many of the typical animals there being rare or wholly absent from other situations. Among all littoral formations there is a more or less characteristic assortment into horizontal zones. In Puget Sound, Shelford (1916) found four zones: (1) shore, between tides, about 3 m. wide; (2) laminarian zone, from low-tide mark to a depth of about 20 m.; (3) coralline zone, 20–100 m.; (4) subcoralline zone, 100–165 meters. King and Russell (1909) on the shores of England at Millport describe the following zones: (1) *Fucus platycarpus* and *Pelvetia canaliculata*, 24 ft. wide; (2) *Ascophyllum nodosum*, 30 ft.; (3) *Fucus vesiculosus* and *F. serratus*, 26 ft.; (4) laminarian zone; (5) coralline zone. On the coast of Algeria, Seurat (1929) recognized three zones: (1) subterrestrial, (2) intertidal, and (3) a stratum not exposed during extreme low tides. On the Washington coast Shelford *et al.* (1935) found four communities: (1) Balanus-Littorina Biome, intertidal; (2) Macoma-Paphia, subtidal on mud bottoms; (3) Strongylocentrotus-Argobuccinum, subtidal on hard bottoms; and (4) Pandora-Yoldia biome, mostly subtidal on soft bottoms. Murray and Hjort (1912) advocate the recognition of a littoral region where there is strong light, 0–30–40 m. in depth, and a sublittoral, 35–150 m. In his study of the Woods Hole region, Sumner (1910) found that depth, as a rule, had little influence in the distribution of littoral animals. He cites one instance, however, where a snail (*Crepidula fornicata*) was confined to the sublittoral zone, although the hermit crab to which it was commonly attached ranged into shallow water. Allee (1923*a*) also working at Woods Hole found the hermit

crab, *Eupagurus longicarpus*, in all types of associations, regardless of the character of the bottom. Huntsman (1918) has shown a very interesting control of vertical migration on the Canadian coast (Fig. 53). He found that where tides ran high Littorina, Balanus, and Mytilus did not extend *below* 4 ft. above

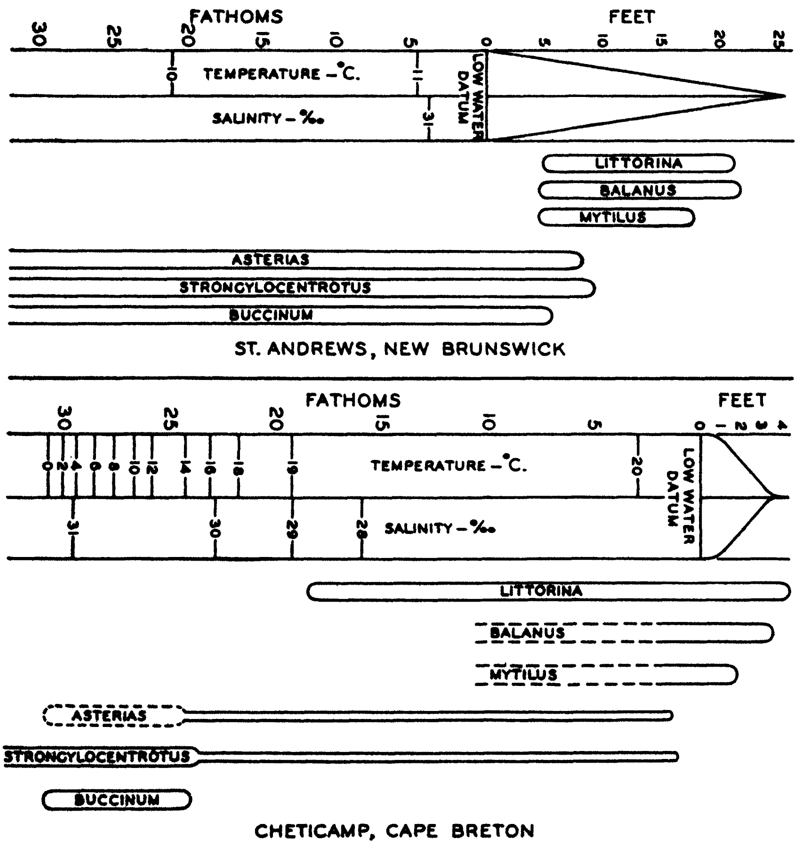


FIG. 53.—Zonations of littoral animals on the eastern coast of Canada. (*After Huntsman* 1918.)

low-tide mark and that this line was about the upper limit of their predaceous enemies Buccinum and Asterias.

The starfish and whelk are enemies of the mussel and it may well be that their presence in abundance near and below low-tide mark at St. Andrews is the determining factor for the lower limit of the distribution of the mussel in that region. The zone of common distribu-

tion is quite narrow—about 3 feet—and does not contain any of these species in abundance. It is to be considered the area of struggle—by the starfish and whelk against the effects of heat and exposure and by the mussel to obtain a foothold in spite of depredations by the whelk and starfish.

In localities where tides were low the snail, mussel, and barnacle extended considerably below low-tide mark. Huntsman also found that barnacles were most abundant where sea urchins were



FIG. 54.—Rocky shore, Nahant, Mass. Snails (Littorina), barnacles (Balanus), and rock weeds (Ascophyllum) are clearly shown.

few or absent. Probably rockweeds attracted the urchins, and localities where they occurred were not particularly favorable for barnacles.

Littoral corals are largely confined to warm seas where they live in rather shallow water with a mean temperature of at least 20°C. Reef builders require higher temperatures. A "coral reef" is built through the cooperative activities of a variety of animals. Certain plants and millipores are binders and shapers, and the corals are fillers. Worms, barnacles, and other organisms also help build (Setchell 1929). It has not been proved that

thick and extensive deposits of ancient limestones were built mainly by corals or algae (Baker 1933).

The most abundant reef builders at moderate depths are madrepores, astraeids, porites, and meandrines. At depths of 90 to 120 feet the millepores and seriastopores predominate. The great field for coral development lies between low water and 120 feet.

Corals are most luxuriant in protected lagoons and channels. McCaughey (1918) described five zones: (1) beach or inshore waters, (2) partially submerged rocks, (3) pools, (4) lagoons, (5) reef rims. Sediments may smother corals (Marshall & Orr 1931). After studying Australian coral growths Stephenson *et al.* (1931) conclude that there is no such thing as a "typical" coral reef. They describe the following zones: (1) dry land, (2) beach sandstone and ramparts, (3) flats and mangrove swamps, and (4) seaward slopes and anchorages.

Adaptations of Littoral Animals.—The adaptations of littoral animals to various peculiar modes of life present an endless variety. There are structures for adhesion, burrowing, resistance to impact, etc. There are animals that feed by spreading a radially disposed group of tentacles, by swallowing mud, by straining microscopic organisms from flowing water, by everting the stomach about the soft parts of some unlucky animal, etc. There are those that escape from watchful enemies by concealing their bodies with coverings of foreign objects or the cast-off shells of other animals and by living in burrows. Sessile animals are protected by hard exoskeletons, nematocysts, avicularia, pedicellariae, and often have special cleaning devices to keep their bodies free from sediment. For reproduction there are adaptations that serve to spread a species or to keep it from being swept out to sea: swimming larvae, adherent eggs, special spawning places, etc. The species of Littorina that live on beaches show an interesting series. Those that live near low-tide mark give off eggs containing earlier veliger stages, and those that live near high-water mark give birth to small snails. Murray (1895) states that animals beyond the mud line (100 fathoms) have no free-swimming larvae and that this fact constitutes a distinction from shore animals. The littoral beach snail in Bermuda, *Onchidium floridanum*, breathes through its skin, except when it is very active in air. It is a pulmonate which has taken up

littoral life, and its lung has apparently become somewhat degenerate (Arey 1936).

On the whole, littoral animals are resistant and capable of enduring wide ranges of variation. Fulton (1921) kept a Bermudan tide-pool anemone in a corked bottle of sêa water without access to the atmosphere for more than 11 days, and the animal was apparently uninjured. He also dried individuals for as much as 6 days, until they had shriveled into a raisin-like mass, but these soon became active when replaced in sea water. Hausman (1920) studied the shore anemone, *Sagartia luciae*, and says:

> It seems remarkable that so soft and relatively defenseless a creature should have so greatly increased its numbers and extended its range in our waters. Its success in meeting the unusually numerous vicissitudes of a littoral existence may perhaps be attributed to the following: (1) an ability to withstand considerable differences in temperature, (2) its ability to withstand buffeting by the waves because of the yielding and resilient character of its body, (3) its ability to contract tightly and to survive through a period of foul water, or of dry conditions exposed to the sun and wind, (4) its apparent disregard of the differences in the salinity of water, (5) its protective coloration, (6) its defensive acontia, (7) its rapid rate of reproduction and growth to maturity, (8) its several methods of reproduction, (9) its ability to withstand annihilation through laceration, and (10) its ability to regenerate lost parts.

Some of the active shore animals are very sensitive to slight variations in environment. Shelford (1915) found that there was usually some hydrogen sulphide on sandy bottoms in the Puget Sound region and that herring usually avoided such localities. Sometimes a storm changed the chemistry of the water, and Shelford believed that herring died on account of such changes. At the time of the great earthquake in 1923 many littoral animals were destroyed along the coast of Japan (Kaburaki 1926).

FORMATION 1. HARD BEACHES

A firm substratum gives littoral animals opportunity to attach themselves. They are thus able to withstand the action of waves and tidal currents and at the same time secure food from the shore algae or from the microscopic life that swarms in littoral water. Hard bottom is usually associated with much movement in the water. The ocean continually sorts over its movable bottom materials, depositing the finest muds at the head of bays

and its sands where there is an intermediate degree of molar activity. Thus the immovable, rocky headlands are left standing out into the open ocean where they receive the maximum of water movement.

Association *a*. Rock Walls

The animals on the unbroken rocky shores of the ocean offer an excellent example of zonation. Highest is the barren transitional strip (Fasciation 1), where neither land nor sea dominates. Here Ligyda, land crabs, birds, ants, and spiders forage over the

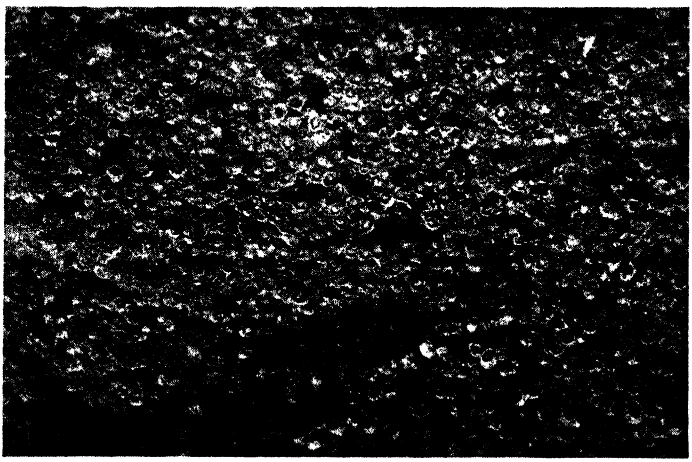


Fig. 55.—Barnacles, Nahant, Mass.

rock surfaces; swallows, dragonflies, and butterflies sail through the air. The rocks in this stratum are not lichen-covered, like those farther inland, but are for the most part bare, thus showing the influence of the ocean. In pools among the rocks little flies (*Coelopa frigida* Falle, etc.) commonly breed. Larvae are often abundant in the water, and the adults may be seen floating about on the surface, often in such numbers as to form veritable miniature rafts. Other insects, such as aquatic bugs and beetles, occur in limited numbers. Earwigs hide in crevices during the day and come out at night to forage.

Intertidal Zone.—The abundant population of the intertidal zone (Fasciation 2) shows an arrangement into horizontal, but more or less overlapping, consocies (Fig. 53). Barnacles extend in a white band usually above other marine animals, but snails

(Littorina) often crawl higher. The water level covers some barnacles only at the time of spring tides, and such individuals have no chance to feed except when, at intervals, food-laden waves dash over them. Yet they cannot move and are able to persist within their calcareous armor. On the rocks at Port Erin, Isle of Man, Moore (1935) found a billion barnacles per square kilometer, and these produced about a quadrillon of larvae annually. Mussels and snails (Littorina) extend as high as the barnacles on bare rock surfaces. In the bands of rockweeds (Fucus, Sargassum, Ascophyllum, Chondrus) many animals find food and shelter. There are chitons, snails (Littorina, Thais, the limpets, Acmaea and Patella, nudibranchs, etc.), clams (Mytilus, Modiola, etc.), sponges, sertularian and campanularian hydroids, anemones, bryozoans, flatworms, annelids (Spirorbis, etc.), amphipods, isopods (especially Caprella and other sedentary types), crabs, sea urchins, starfishes, attached ascidians, fishes, and other animals. Even some crinoids are found between tides (Clark 1921). Arey and Crozier (1921) have described an interesting society on the Bermuda coast where snails (*Onchidium floridanum*) live in little crevices and come out for only about one hour out of each 12 to feed on algae. The species of snails of the genus Littorina that live on rock beaches, though much alike in structure, occupy separate zones—being assorted according to their adaptations to plants, crevices, and sunlight (Haseman 1911. Flattely & Walton 1922, Colman 1933, Hewatt 1937). Figure 56 shows a marked arrangement of intertidal animals in rather definite strata. On the coast of British Columbia, Saunders (1928) found 12 species of dipterans and beetles which lived in the intertidal zone as larvae or adults and were able to endure immersion in sea water.

Laminarian Zone.—In the Laminarian Zone (Fasciation 3) below the low-tide mark there is a characteristic group of species. Here lobsters and other animals that do not migrate up into the intertidal zone are often associated with barnacles, mussels, snails, and other species that also live at higher levels. Certain species move up somewhat with each rising tide (sea urchins, starfishes, crabs, carnivorous snails) and drop back with the ebb. Murray and Hjort (1912) have pointed out that *Laminaria hyperborea*, which has stiff stalks, shelters many animals, whereas other laminarians with thin, pliant stalks support few attached species.

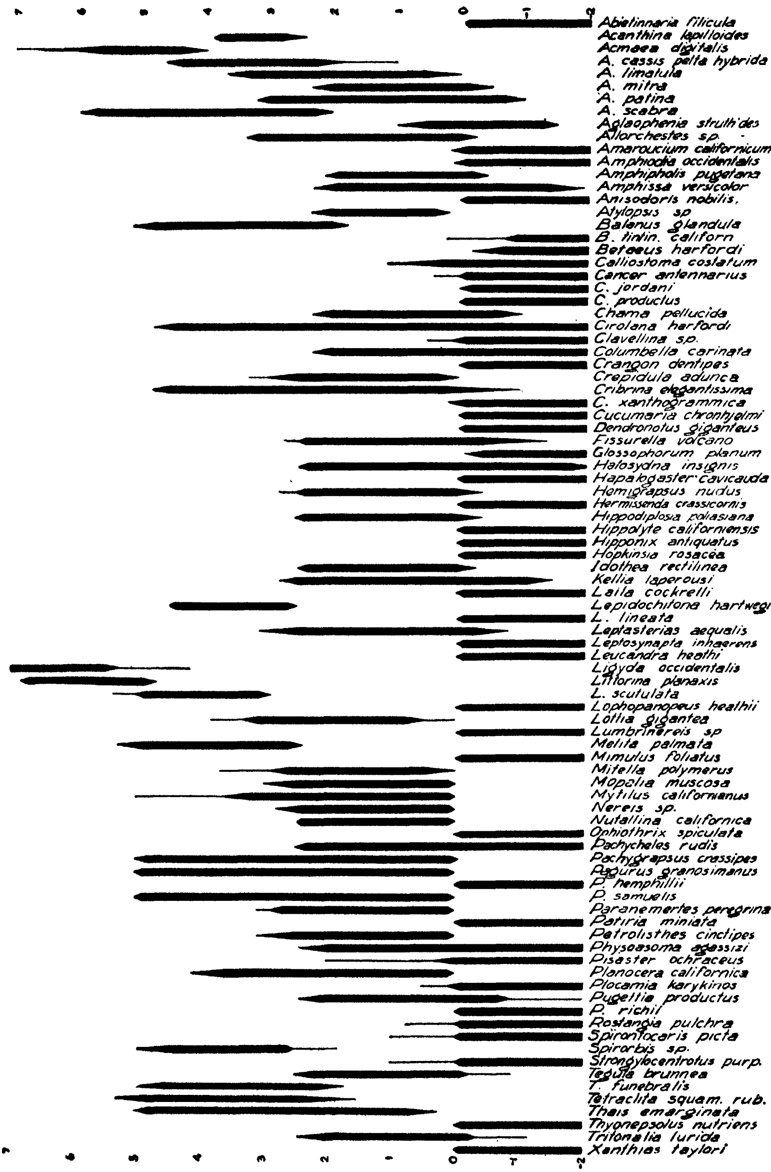


Fig. 56.—Vertical distribution of animals on rock beaches at Monterey, Calif. (*From Hewatt* 1937.)

Shorewater.—The shorewater (Fasciation 4) has a characteristic fauna and flora which is in many respects distinct from that of the open ocean. Some of the animals are free-swimming stages of species which live on the shore during parts of their lives. Crabs and starfishes have swimming larvae; many attached hydroids bud off sexual medusae, which, in turn, often produce swimming planulae. The organisms of the shorewater constitute the sole food of many of the attached animals along beaches.



FIG. 57.—A sea urchin (Strongylocentrotus) that had remained on one spot so long that a sponge had grown up around it.

Adaptations of Animals on Rock Beaches.—Marine rock beaches furnish an abundance of food, but conditions of life on them are severe. Many of the animals are firmly attached in order to withstand the continual movement of waves and tides. Radial symmetry is usually associated with attachment, and many of the animals show it. Even animals that are able to move about do so very little. The snail Thais is quite sedentary. Individuals may be born at a certain level and remain there all their lives. Some of the individuals that live above high-tide mark lack opercula (Colgan 1910). The writer (1914) once found

a sea urchin that had rested so long in one spot that a sponge had grown up and inclosed it in a living nest (Fig. 57). He also mapped a colony of anemones in a beach pool, carefully plotting the position of each individual, and found that after two weeks not one could be observed to have moved. Some limpets remain on one spot so long that they wear scars in the rocks. Many rock-beach animals are protected by the hard shells that cover their bodies (Fig. 58). Parker (1917) found that a beach anemone (Cribrina) held bits of shell about its column by means of sucking disks to protect itself from the beating of the waves. Other animals escape the impact of waves through their small



FIG. 58.—A crab, *Grapsus grapsus*, that runs about on rock walls where waves beat.

size, which enables them to creep into crevices. Arey and Crozier (1921) found that Onchidium never emerged from its home crevice when the tide was in. Hamilton (1903) observed an interesting type of behavior in a chiton that lived in cavities in coralline rock on the coast of Cuba. These molluscs crouched against the rock when a wave came in but raised their bodies and allowed the water to run over their gills when it receded. Their eyes apparently served to give notice of coming waves. Some animals escape wave action by boring into the rock itself. An isopod (Sphaeroma) and clams tunnel into rocks on the coast of Australia (Stead 1900); a clam known as the "piddock" establishes itself for life in the rocks along the Pacific coast of North America (M'Curdy 1902); in the Atlantic, rocks are excavated by sea urchins and clams. Even some of the classic buildings along the

Mediterranean have been bored into by clams at times of high water.

The animals remaining above low-tide mark show various adjustments to resist the drying action of the atmosphere while they are exposed. Barnacles and molluscs are protected by their calcareous shells and opercula; anemones are turgid with water when the tide goes out and gradually become flaccid; many smaller animals hide under the rockweeds; some secrete slime which serves as a covering for the body; certain crabs, starfishes, and other motile animals cannot long endure desiccation and therefore must migrate downward when the tide ebbs. Acorn barnacles, *Balanus balanoides,* often grow faster and live longer at high levels on rock beaches (Moore 1934). They depend on the ocean for food but flourish near high-tide mark. At low tidal levels, barnacles attain sexual maturity earlier than at high levels. Growth is most rapid where there is greatest exposure to waves (Moore 1935).

Rock-frequenting littoral animals have various means of adjustment to the temperature changes. Skeletons, slime, water loss, nocturnal habits, and instincts to seek shelter serve to mitigate the heat of summer. During the winter many unattached shore animals move into deeper water. Some of these are able to respire from either water or air.

Origin of Littoral Fauna.—The invasion of littoral habitats has not come altogether from the ocean. King (1914) described several species of mites that are adjusted to rocky shores and show varying degrees of ability to endure submergence. Podurans and halobatids have also been derived from the land. The strenuous existence that shore animals are obliged to lead apparently has some compensation. Hubbs (1920) affirms that reef fishes usually have few parasites and he believes that this is "a fact apparently due to the strength of wave and tidal currents."

Feeding of Animals on Rocky Shores.—The feeding of the animals on rocky beaches is more or less characteristic. Those that are attached spread sweep nets (barnacles) or tentacles (hydroids, anemones, bryozoans) or siphon water through their bodies (clams). It is not safe for any microscopic organism to come near the living blanket on a rocky shore. Snails, sea urchins, and other algal feeders search over the rocks or lurk in favorable nooks. Ribbon fishes, sculpins, small crustaceans,

crabs, drills, and starfishes commonly seek their prey when the tide is high and hide away when conditions for feeding are not favorable. Cribrina captures food with special tentacles which are provided with sucking disks. Onchidium emerges from its home crevice for only an hour each day when the tide is out but in that time rasps enough algae off the rocks to sustain it. Crozier (1921) summarizes estimates concerning the amount of water



FIG. 59.—Animals in a rock pool.

siphoned daily through certain rock-beach animals as follows: one sponge "finger," 78 l.; Ascidia, 173 l.; Stichopus (for respiration), 20 l.

Animals in Pools on Rocky Shores.—Rock pools are frequently carpeted by living animals. Certain sponges, hydroids, anemones, bryozoans, crustaceans, clams, snails, ascidians, and fishes flourish in such situations. The shanny, blenny (viviparous), lumpsucker, gunnell, 15-spined stickleback, and five-bearded rockling, which live in pools along the British coast, produce many eggs or young because so many are destroyed, particularly by predaceous enemies (McIntosh 1900). The young of the Californian viviparous perch leave the lower beach pools soon

after hatching and remain in those at higher levels, where they are secure from predators and are inundated only at high tide (Hubbs 1921*a*). Klugh (1924) has made a careful study of six beach pools on the rocks of the New Brunswick coast. These were much alike except for their elevation, constituting a comparable but graded series. There was a change in salinity in the higher pools on account of evaporation. The chemical nature of the water was found to be influenced largely by the plants present. Temperature varied widely. In the lower pools it was never above 3°C.; in the highest, it rose to 15–28.5°C. A fauna characteristic of the laminarian zone was found in the three lower pools but was absent from those above. This was associated with coralline seaweeds. Algae in a rock pool may increase the oxygen by photosynthesis. At Tortugas the writer (1929) found that temperatures seldom were as high as 38°C. in small, sunny, rock-bottomed pools in which hermit crabs, crabs, and snails were living.

Association *b*. Pebbly Beaches

Loose pebbles on a rock beach may change the character of the fauna. Usually, there is an increase in the number of animals that frequent crevices. Sumner (1910) found that the distribution of *Thuiaria argentia* was confined to situations where there were loose stones. The Basque coast lacks the zonal arrangement characteristic of that along Brittany on account of the presence of pebbles and warmer water. On the former, nullipores, sea urchins, and anemones are dominant types (Beauchamp 1907).

Association *c*. Piles, Wharves, and Ships

The wooden structures introduced into the ocean by man are populated largely by animals that frequent rocky shores (Fig. 60). Wood, however, is frequented by certain boring animals that do not work in rock. On the exposed surfaces (Fasciation 1) are barnacles, hydroids, corals, sponges, oysters, amphipods, isopods, spider crabs, mussels, snails, and ascidians. Tunneling in the wood (Fasciation 2) are shipworms (Teredo, etc.) and the crustaceans, Chelura and Limnoria. These animals are very destructive and cause great economic losses. The shipworms are highly adapted to the life that they lead. They react to unfavorable

chemical changes in the water around them by drawing in their siphons and closing their tubes with their pallets. In this condition they may remain quiescent for as long as six weeks. They bore actively at temperatures between 5 and 27°C. The shipworm near Seattle, *Bankia setacea,* attacks timbers most



FIG. 60.—A group of animals associated with wharf piles. (*From Miner* 1913, *courtesy of the American Museum of Natural History.*)

when temperatures are between 7 and 12°C. It is prevalent just below the tidal zone. Limnoria is most active in spring and most often below low-tide mark. Tubicolous annelids and bryozoans are active in autumn and are also most abundant at lower levels (Johnson & Miller 1935). Shipworms are able to subsist on wood alone for a year or more, but they also feed on

plankton, which is drawn through their incurrent siphons (Roch 1932). Their burrows are lined with calcareous secretions. Both boring crustaceans and molluscs are more abundant in the lower half of the intertidal zone or below it.

FORMATION 2. SHIFTING BEACHES

Beaches that have shifting substrata form a graded series with firm clays at one end and at the other soft muds which occur on shores where sediment is accumulating.

Association *a*. Clay Beaches

Although clay bottoms are hard enough to give a firm foothold for clinging animals, they do not permit permanently attached animals, like barnacles, sponges, and hydroids, to exist. There are, however, creeping types, such as snails and chitons, which are often common, particularly in crevices and eroded holes. The drift line (Fasciation 1) here supports the usual group of scavenger insects, but the small amphipod crustaceans are not abundant, as on sand beaches. The intertidal zone (Fasciation 2) is usually dominated by crabs, which find an excellent place for their burrows in the clay because it does not cave in readily. The zone below low-tide mark (Fasciation 3) is similar to that on rocky shores, but patches of mud and eelgrass often occur.

Association *b*. Sand Beaches

Sand beaches occur where there is considerable water movement and therefore, although they are made up of particles that are less transportable than the fine sediments that are found in mud, are the most unstable of shore bottoms. There is much variation in the mineral and organic contents of beach sands. Along the eastern coast of the United States calcium carbonate varies from 0.0–100.0 per cent (Hamaker 1930). Few algae can maintain themselves, though there are some that live in or on the sand. Spermatophytes that are provided with roots or rhizomes are quite characteristic in certain situations though usually not abundant. Both plants and animals are more abundant on sheltered than on exposed beaches. Many of the latter live below the surface of the sand, and special adaptations for respiration and feeding are often present. In speaking of

adaptations that certain crustaceans have for keeping sand from entering their branchial chambers Garstang (1896, 1898) says:

> It is both remarkable and interesting that the same function in relation to the process of respiration should be discharged by organs and parts so dissimilar from one another as are the first antennae of *Abunea*, the second antennae of *Corystes*, the frontal area of *Platyonichus nasutus*, the five lateral spines of *Atelecyclus*, the crests of the chelipeds of *Calappa granulata*, and the orbits of *Matuta victor*.

Drift Line.—High up on the beach in all warm parts of the earth live the crabs of the genus Ocypode. They are well protected by their resemblance to the sand and, as they scuttle for

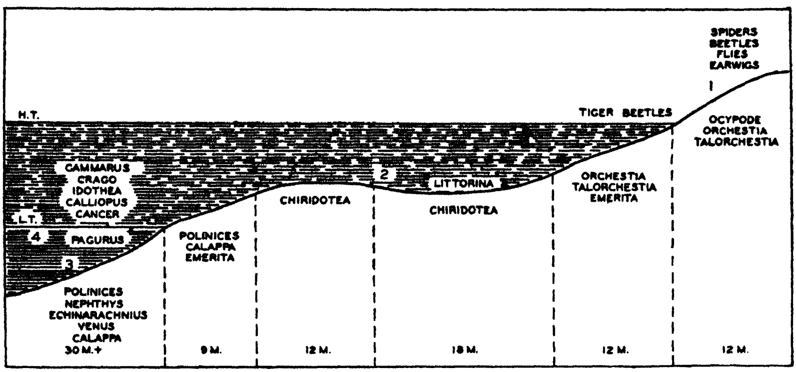


FIG. 61.—Section of a sand beach showing usual positions of characteristic animals, east coast United States.

their burrows in the twilight, are well named "ghost crabs." Along the drift line (Fasciation 1) are myriads of sand hoppers (Orchestia, Talorchestia, etc.) and scavenger insects (flies, beetles, ants). Sand spiders, tiger beetles, and robberflies seek their prey on the smooth stretches of sand. Great turtles come from the open sea and climb out on sandy beaches to lay their eggs above high-tide mark.

Intertidal Zone.—The intertidal zone (Fasciation 2) shows a variable stratification depending on the exposure of a beach to the open ocean. Very often where there is a rather steep slope there is little life below the drift line. Below this there is a rather flat, ripple-marked zone where the tortuous tracks left by the little isopod Chiridotea are found. Chiridotea is extremely flat and can slide in and out of or through the sand with great ease.

Where there are plants growing so that roots hold the sand together, the burrows of fiddler crabs may be found. Below the flat there is often a little barren ridge which is covered with small pebbles. On the seaward side of this are little V's made by the antennae of the mole crabs (*Emerita talpoidea*, etc.), which protrude above the sand into the receding waves. Beyond that ridge a gentle grade leads into deep water. On this slope are many characteristic sand-dwelling animals. When the tide is in, shrimps swim about or scamper over the sand and burrow, so that their bodies are partly buried. In the tropics the crabs of the genus Mycteris dig their holes near low-tide mark and remain buried while under water. Hermit crabs and isopods (Idothea) move up and down with the tides. Flat coral sand contains few interstices between its grains; but coarse sand gives shelter to a whole group of characteristic species of copepods, which Wilson (1935) calls "terraqueous." They are adapted for burrowing. Haustorius and other burrowing amphipods share the sand with sea cucumbers (Synapta), enteropneustans, lancelets, worms, (Arenicola, etc.), sand dollars, spatangoids, sand snails (Lunitia, Fulgur), and clams. In some parts of the world the beautiful Renilla buries itself when the tide is out and expands when it is again covered with water. The snails slide through the submerged sand and burrow in when waves begin to shift it about. Several make peculiar egg cases by fastening the sand together with slime. Some annelids also anchor cocoons of agglutinated eggs in the sand. A sipunculid worm which lives on sandy California beaches is very hardy. It can live a week without oxygen and may lose as much as 50 per cent of its body weight by desiccation and survive (Peebles & Fox 1933). Perhaps the clams (Venus, Cardium, Ensis, Solen, etc.) are as characteristic as any group on sand beaches. Their heavy, well-protected bodies and burrowing ability enable them to live in the shifting substratum with little danger of injury, and their siphons permit them to obtain food from the water. The synaptas lack respiratory trees and burrow at some little distance below the surface. The sand-dwelling echinoderms are also highly adapted; the flatness of the sand dollars enables them to slide through the sand and offers little surface for wave action; the spatangoids can remain largely below the surface and feed through the activities of the "brushes" on the petaloid ambulacra

which lie on the upper side. Exposed sandy beaches in the intertidal zone may become warm or cold but at depths of 8–15 cm. temperatures are relatively stable (Newcombe 1935).

Below Low-tide Mark.—Below low-tide mark (Fasciation 3) lurk rays, flounders, sand eels, and other animals which move up the shore with each tide in search of food. On sandy shores there is a rather gradual transition into deep water, and many of the littoral animals (Venus, sand dollars, spatangoids, etc.) extend to considerable depths. Allee (1923) notes that in the Woods Hole region a worm, *Scoloplos fragilis*, is the dominant species on sand bars that lie offshore. The shorewater (Fasciation 4) contains the usual store of floating and swimming organisms which are, living and dead, the most important source of food for sand-beach animals.

Association *c*. Mud Beaches

Mud is deposited on beaches where the action of molar agents is not pronounced. The animals that live in the mud itself are chiefly burrowers which, on account of the stagnant medium in which they live, are commonly provided with special means for creating respiratory currents. Many have hard exoskeletons or build tubes. Sumner (1910) in his extensive survey of the Woods Hole region found a greater number of species on rock and gravel bottoms than on mud. Allee (1923) asserts that the fauna of mud flats differs markedly from that on other types of beaches. He says: "The associations of the flats are highly independent of others." On the coast of England Elmhirst (1932) counted animals at various levels on sand-mud beaches. A little clam, *Tellina tenuis*, averages as follows per square meter: high-tide mark, 528; half tide, 1,892; low-tide mark, 44. At one place in Zostera beds there were per square meter: 50+ *Littorina littorea;* 24,000–32,000 nematodes (mostly *Einoplus communis* and *Oncholaimus* sp.); 20,000–48,000 olgochetes (mainly *Tubifex costatus* and *Peloscolex benedeni*); and 6,000–8,000 polychaetes (largely *Amphicora fabricci*). In clean sand near low-water mark there were in 1 sq. m.: 252 *Ampelisca laevigata*, 1950 *Corophium crassicorne*, 740 Bathyporeia, and 174 Urothöe.

Drift Line and Flats.—The drift line (Fasciation 1) on mud beaches has a population of scavengers, with fewer amphipods than on sandy shores, and there are usually few or no algae.

Below this the bare mud flats (Fasciation 2) are spread out. The surfaces of these get very hot in the sun, but colonies of

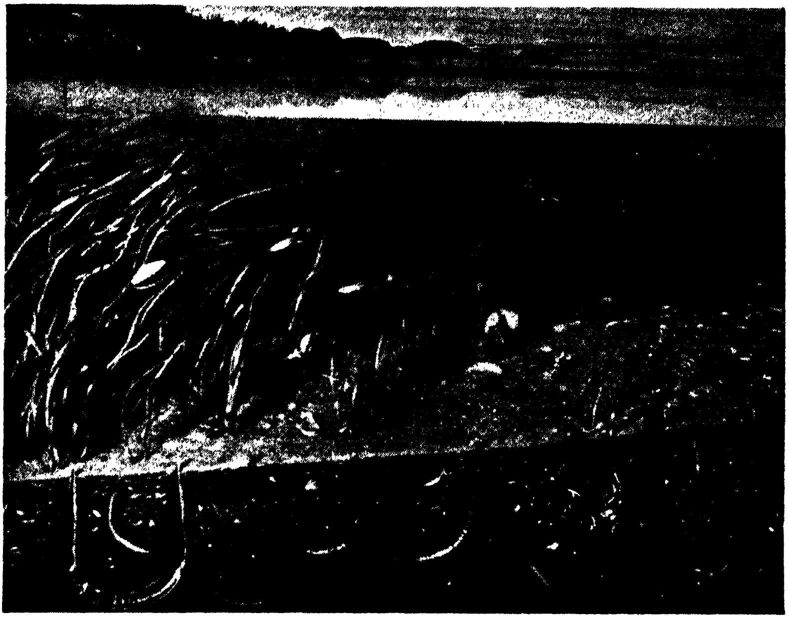


FIG. 62.—Section of fasciations 2 and 3 on a mud beach. (*After Miner* 1912, *courtesy of American Museum of Natural History.*)

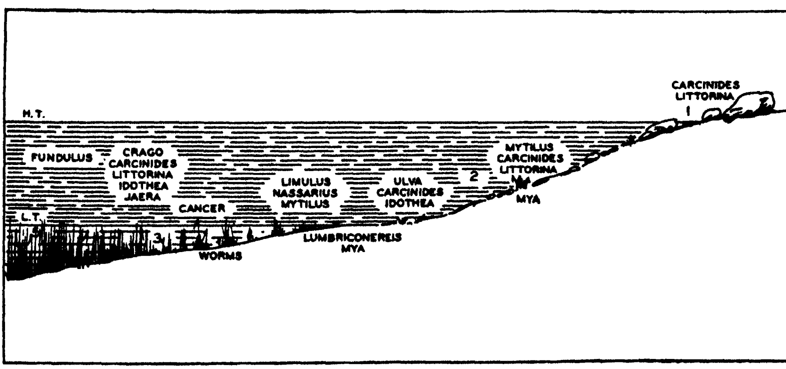


FIG. 63.—Section of a mud beach, showing usual positions of animals, New England coast.

mussels, by attachments to each other, often form great rafts and appear to flourish. In the mud, worms, the clam Mya, and the brachiopod Lingula are characteristic. The Japanese

Lingula never invades sandy or plant-covered areas (Yatsu 1902). This animal retreats as deeply as possible by contracting its peduncle when the tide is out. The peduncle is not attached but is so firmly imbedded in the mud that it is often broken when the body is pulled out. Lingula makes burrows by squirting water and rubbing slime along the walls of the cavity thus formed. It has great resistance to stagnation. One colony described by Yatsu survived when all molluscs were killed. Where stones or drift are present on flats, worms or other animals commonly burrow under them; barnacles, snails, and other



Fig. 64.—A pair of king crabs (Limulus) spawning on a mud beach. Only the male is seen, as the female is buried beneath the surface.

hard-beach animals may also find attachment. On the coasts of Siam there are three species of beach slippers (gobies) which live together on tidal mud flats. These fishes differ in food habits, and hence there is little competition among the species (Pearse 1933).

Low-tide Mark and Below.—Near low-tide mark, sea lettuce (Ulva) and eelgrass (Zostera) begin, and a little below this the latter forms a dense growth (Fasciation 3). The mud snails (Nassarius, etc.) and often fiddler crabs are found somewhat above the vegetation zone, and many nematodes, annelids, and clams flourish among the roots. On the coasts of Japan a small cuttlefish adheres by its ventral surface to the underside of Ulva fronds. It holds its tentacles together and keeps turning its head

about to observe passing animals that it may capture for food (Sasaki 1923). There is an abundant population among the eelgrass leaves. Along the borders of open spaces starfishes pursue scuttling scallops, and holothurians (Thyone, etc.) wave their tentacles. Hermit, rock, spider, and panopeid crabs scamper about seeking food. The eelgrass serves to support snails (*Littorina minuta*, etc.), tubicolous worms (Spirorbis), and certain hydroids. The gigantic hydroid Corymorpha imbeds its stalk in the mud. Where there is a current, passing particles are captured for food; but in quiet water the stalk is bent over, and the tentacles are scraped over the bottom. On the Australian coast, according to Dexler and Freund (1906), the dugong does not frequent estuaries but browses on eelgrass along the borders of muddy shores. Fishes like Fundulus, pipefish, eel, and stickleback migrate back and forth with tides. Jackson (1922) says that eels, Funduli, and young flounders burrow into the mud at the bottom of puddles when left stranded by the tide and thus survive until the water covers them again. The toadfish nests in such situations as old cans and hollow logs on mud beaches. The male clears off his nest and continually fans it to keep the eggs clean. He induces as many passing females as he can to deposit eggs. When the tide is out herons, gulls, snipes, crows, and other birds often resort to the flats to feed. On shores where there is an intermediate degree of wave and tidal movement there may be a sand beach in the upper strata followed by eelgrass and characteristic animals of Fasciation 3 of mud beaches.

Lagoons.—Lagoons (Fasciation 4) usually have a muddy bottom and have a characteristic fauna of anemones, holothurians, worms, molluscs, and other animals. Crozier (1918) has estimated the amount of mud (dry) that passed through a Stichopus at 6–7 kg. each year. The digestive secretions of this holothurian are acid enough to dissolve some calcium carbonate, but little grinding action is exerted on particles that pass through the gut. McClendon (1910) found that many of the animals in the lagoons behind coral reefs were negatively phototropic and positively thigmotropic.

Shorewater.—The shorewater (Fasciation 5) near mud beaches varies considerably in its temperature and gas content. When the tide is out, water standing over vegetation may become very warm and supersaturated with oxygen, whereas water over masses

of drift may have an unusual amount of carbon dioxide. The rising tide, however, usually mixes the water and soon brings it to a condition of chemical and thermal uniformity. Eelgrass that is out of water at low tide serves as a mat to protect animals beneath it.

Association *d.* Estuaries and Sounds

The vegetation of brackish water is closely allied to that on marine shores but, depending on its salinity, "also includes other species and genera, such as Chara, Zannichellia, Batrachium, Naias, *Potamogeton pectinatus*, and Myriophyllum, which reappear more bountifully in freshwater" (Warming, 1909).

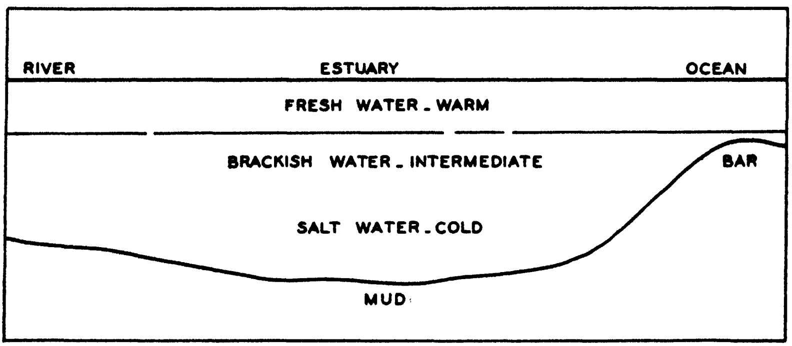


Fig. 65.—Diagram of stratification at the mouth of a river.

Murray (1914) estimates that about 3.7 cu. miles of suspended and dissolved material are carried into the ocean each year by rivers. At this rate the whole of the present land volume would be carried away in 6,340,000 years. The salts in rivers are principally carbonates, and the salinity averages about 0.018 per cent (ocean, 3.5 per cent). The eggs of *Littorina litorea* (L.), a common beach snail, may live in salinities of 10–15 but cannot develop; above S15, development may proceed slowly; but normal growth takes place only when salinities are above 20 p.p.m. (Hayes 1927).

Stratification.—At the mouths of rivers there is usually a transition in temperature and salinity which leads to a stratification of the water. At the mouth of the St. Lawrence River, Huntsman (1918*b*) found three layers: (1) a warm surface layer—a mixture of river water and warm ocean; (2) an intermediate

layer (18°C.); and (3) a cold (0°C.) layer near the bottom. The fishes were arranged in five zones: (1) In deep channels were few fishes, rockling, angler, skate, sole, etc.; (2) banks were covered with ice-cold water and were resorts for plaice, sole, skates, cod; (3) the warm surface water contained dogfish and mackerel in the open and, alongshore, cunner, grubby, eel, sand flounder, pipefish, young sand flounder, butterfish, smelt; (4) in the intermediate zone herring ranged in the open, and on the bottom were haddock, hake, dab, adult flounders, muttonfish, wolf fish, sculpin, and skates; (5) in the estuarine transition from shorewater to fresh were the smooth flounders, white perch, sand smelt, Fundulus, and stickleback. The important zones for

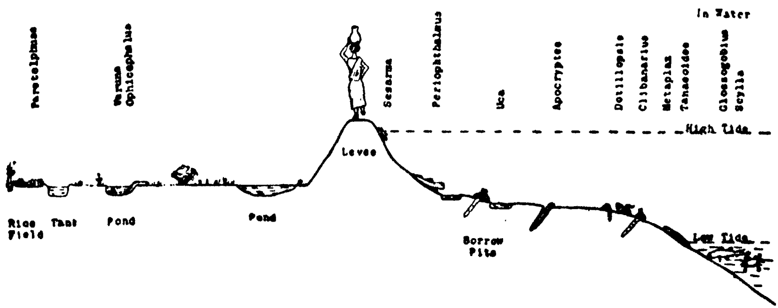


FIG. 66.—Arrangement along a bank of the Matla River in the Ganges Delta. (*From Pearse* 1932c.)

food fishes were the third and fourth. The writer has observed similar stratification in estuaries of the Tonegawa in Japan and the Apalachicola River in Florida. The flowing of tides over bars at the mouths of estuaries may produce vertical circulations which bring cold water to the surface (Huntsman 1923).

Murray and Hjort (1912) describe the "pools" at the mouths of rivers in Norway as ranging up to 30 m. in depth. The surface is covered by a layer of more or less fresh water. "About 1 to 2 meters below the surface the temperature in some summers may rise to 30°C., or even more, while that at the surface does not rise above 18 to 20°C." In such pools live oysters, scallops, anemones, starfishes, crabs, and mussels—the fauna as a whole being "decidedly southern" in its relationships.

At the mouth of the Caspian Sea, Tschugunoff (1921) finds three strata: (1) an upper layer with less than 0.75 g. of sodium

chloride per liter, (2) a brackish layer, ranging up to 3 g. per liter, (3) a salty layer, ranging up to 4–16 g. per liter. In this case the plankton organisms are assorted according to salinity. Fifty-two of the 92 species recorded are characteristic of fresh-water. The salinity of Chesapeake Bay increases downward, with a rapid rise at a depth of about 10 m. (Cowles 1923).

Zonation of Estuarine Animals.—Ferronnière (1901) made extensive studies of the distribution of the plants and animals at the mouth of the Loire. He found that in going upstream representative marine plants and animals dropped out in the following order: *Arenicola marina, Lineus gesserensis, Carcinas maenas, Sphaeroma serratus, Fucus* and *Lichina, Balanus, Amphitrite, Cardium edule, Heterochaeta, Vermiculatus, Phragmites communis, Boccardia ligerica, Nereis diversicolor, Palaemon edwardsi.* This writer notes that when salinity changes there may be various responses, which he lists as follows: (1) immediate death; (2) autotomy; (3) violent contractions or irregular movements; (4) tropisms, etc.; (5) exaggeration of certain natural functions; (6) establishment of a new equilibrium; or (7) acclimatization without observable change.

Variations in Salinity.—There have been many studies upon the ability of estuarian animals to survive changes in salinity. Packard (1918) investigated 23 species of lamellibranchs and 12 species of snails in San Francisco Bay. He concluded that depth had little influence on distribution but that the character of the bottom was of great significance. Low salinity and wide ranges in salinity were unfavorable. The shipworm (Teredo) readily survives rapid changes in salinity (Blum 1922). It will remain active in water that contains 9 g. of salt per liter but dies when there is only 5. It may close its burrow with its pallets and thus retain salty water within for a time. At Tortugas, Fla. (1929) and Beaufort, N. C. (1936), the writer tested the toleration of 66 littoral and estuarine species for dilutions of sea water. Among these none lived longer in fresh water than in sea water; seven appeared to be adapted to brackish water, but the others were marine. At Beaufort the abilities of 25 estuarine species to endure desiccation were tested. Types that appeared to be most resistant were those accustomed to spend much time out of water and those with thick protective shells. In brackish pools along the Sussex Coast, Thorpe (1927) observed that certain marine

species were smaller in size when in lower salinities and attributed the condition to lower metabolic rate; but as Schlieper (1933) has pointed out, animals have to work harder to respire in fresher waters. Few marine animals appear to have migrated through estuaries to attain life on land, but many have gone from the ocean directly over the beaches. Difficulties encountered in estuaries are concerned chiefly with salinity, respiration, and



FIG. 67.—Mangroves on the coast of Colombia.

reproduction. Some estuarine animals show adaptations for burrowing (Eupogebia) and toleration of low oxygen concentrations (toadfish); others are active and euryhaline (Callinectes). Fresh water flowing over tidal sands does not penetrate to a depth of more than about a foot; burrowing marine animals may therefore persist in estuaries (Reid 1932).

Oyster Typical in Estuaries.—Nelson has written a number of papers on the oyster. He has found (1921, 1935) that oysters eat a variety of plankton, 80 per cent of animal food being taken at times. An oyster strains about 26 l. of water per hour, or about 360 l. per day in summer. It is active about 14 or more hours out

of each 24; 73 per cent of shell closures are during ebbing tides, and 50 per cent between 11 P. M. and dawn. When the density of the surrounding water reaches 1,008 the shell closes but opens again if the density is raised to 1,010. In another paper Nelson (1923) states that there is a sudden decrease in ciliary action between 4 and 6°C. and that below 4°C. there is no feeding. There is active feeding as the tide rises, and little as it falls. For oysters that have been living in water of fairly constant saline content there is a definite minimum salinity below which the bivalves become inactive. This minimum salinity is lower for oysters grown in brackish water than for those matured in waters

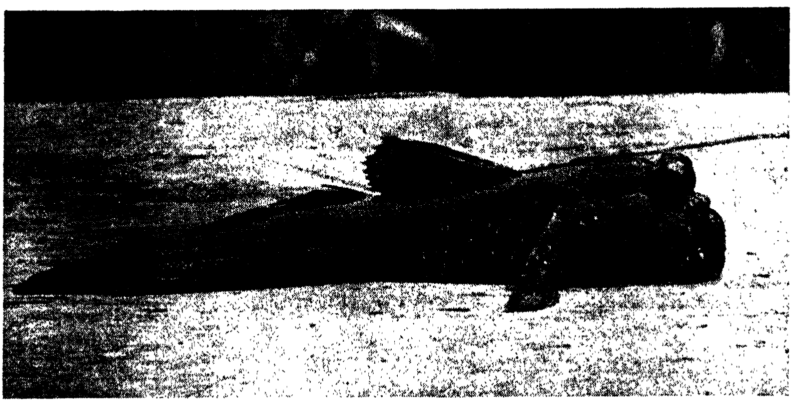


FIG. 68.—Fish, *Periophthalmus kohlreuteri*, that climbs about on mangrove roots and has eyes adapted for vision in air, Nigeria.

of higher salt content. Oysters continue to feed when the water surrounding them is very turbid. In Galveston Bay, Hopkins (1931) found that young oysters would not become attached during periods of low salinity. Apparently larvae require at least about 20 g. of salt per liter to grow and set.

Fishes of Estuaries.—The male gafftop-sail catfish carries eggs in his mouth and goes without food for 80 days (Gudger 1912). "The habit is common to estuarine catfish in all tropical and warm temperate regions." The eggs are thus protected from predaceous enemies and are in no danger of being smothered in mud. On tropical mud flats gobies are characteristic (Pearse 1933, Panikkart Aiyar 1937).

Plankton in Estuaries.—Near the ocean the amount of plankton in an estuary may vary with the flow of tides, increasing

with the flood and decreasing with the ebb (Smith 1933). This is in part due to the mixing of fresh and salt waters.

Bays Resemble Estuaries.—What has been said of estuaries often applies in a general way to bays. Nelson (1917) noted that oyster larvae were numerous at the heads of bays and that, though they were swept back and forth by tides, few were carried out to sea. He (1923, p. 33) has advanced the theory "that oyster larvae work back toward the headwaters and away from the sea by rising on the flood tide and sinking on the ebb." Murray and Hjort (1912) note that in Norwegian fiords the limpet and Purpura are absent and hydroids decrease away from the ocean. They believe this to be due largely to decrease in salinity, which is especially marked along the shores and less marked in deeper water. Near Misaki, Japan, the headlands are covered by barnacles and vermetid snails (Thylacodes), but at the heads of the narrow bays these animals are wholly absent and are replaced by snails (*Littorina brevicula*). Chesapeake Bay has been studied by Cowles (1930), who gives lists of animals and plants present and an analysis of environmental conditions in relation to productivity.

Association *e*. Marshes

Marshes resemble estuaries in that they are transitional regions between salt and freshwater. Warming (1909) says that marshes "are not only floristically, but also anatomically and morphologically so peculiar, that they differ widely from fresh-water swamps."

Mangroves.—Perhaps the most characteristic and extensive of the marshes in tidal waters are those formed by mangroves on flat, muddy shores, especially in lagoons near the mouths of rivers and in estuaries. Mangroves are specially adapted to live on soft, mucky, poorly aerated bottoms. They possess prop and respiratory roots. Their seeds germinate into a spike while still attached to the stem on which they grew and, when ripe, fall and plunge into the soft substratum where they are not readily dislodged. Mangroves are usually densely populated by crabs which dig burrows among the roots. Gobies also climb about on their roots in many localities. Their branches are favorite roosts and nesting sites for herons and also shelter deer, raccoons, and other animals.

Animals of Marshes.—Marshes in temperate regions furnish habitats for characteristic birds, such as bitterns, rails, snipes, grebes, and ducks. Their seaward margins are inhabited by sand hoppers, fiddler crabs, marine snails, and clams (Nassarius, Mya). Where their inner margins grade into freshwater there may be such types as cattails and pond snails. Areas like those along the coasts of Carolina, Florida, and Louisiana extend over many miles through which transitions from salt to freshwater faunas may take place. Probably animals in such areas are acquiring new limits of toleration, and perhaps through the ages such new modes of life may become hereditary. Certain mosquito larvae and dragonfly nymphs are known to be able to live in brackish water (Pearse 1932). In a marsh near Edinburgh, Nicol (1935) studied animals in relation to salinity, oxygen, alkali reserve, ionization, and temperature. Such factors were found to vary greatly with tides and changing weather conditions, but the animals were little affected except in pools of low salinity, where the fauna was largely derived from freshwater. A sudden increase in salinity exterminated such animals, and they were replaced gradually from neighboring ponds as the salinity decreased. The distribution of species in saltier pools was found to depend on the nature of the bottom and the presence or absence of diatoms and other algae. In Italy, Zanco (1932) found that diurnal variations in pH were greatest in marsh pools where salinity was low and where many organisms were present. In speaking of the marshes along the shores of New Jersey, Martin (1923) emphasizes the importance of land organisms and those from landlocked waters as sources of food for oysters. He says:

> The marshes adjoining Barnegat Bay are covered with a dense growth of *Spartina glabra* and associated plants and scattered among them are numerous shallow salt ponds, the larger of them connected by creeks with the lagoons or the bay. The striking feature of these ponds is the extreme abundance of plankton in them even as compared with the rich waters of the bay, which makes them important sources of oyster food. The bearing of this fact upon the adjoining waste land to the oyster beds, and especially the possibility of increasing the supply of oyster food by appropriate treatment of the land-locked waters, is obvious.

In the Hebrides Islands Nicol (1936) investigated a series of small lakes in which pH ranged from 5.4 to 7.8–9.9. The fauna

was varied: 59 marine, 24 freshwater, and 25 brackish water species were found, as well as 5 euryhaline species. Pools in sandy islands at Dry Tortugas, even when quite close to the ocean, maintain salinities much below that of the water in the neighboring ocean. Such pools are quickly invaded by aquatic insects. More or less euryhaline marine types such as Calianassas, snails, mullets, and needlefishes are associated with dragonflies, water boatmen, surface bugs, beetles, and midges (Pearse 1932*b*).

PROVINCE B. PELAGIC

The flora and the fauna of the open ocean are at the same time primitive and specialized. The plants are all algae, and microscopic unicellular species greatly exceed in quantity the multicellular types. Indeed, all the multicellular pelagic algae are derived from the shore. The gulfweed, *Sargassum bacciferum,* and the rockweed, *Ascophyllum nodosum,* which cover great areas in the middle of the Atlantic, grow to some extent after they separate from their shore attachments, but they do not form new bladders, hence gradually sink and after a time contribute their substance to bottom sediments or furnish food for animals below the surface (Murray & Hjort 1912). Arnold (1901) affirmed that of the hundred odd species in the genus Sargassum only *S. bacciferum* is found in the open ocean.

Types of Plankton.—Pelagic organisms are often divided into plankton, which includes those that float or swim feebly and are carried about by currents; and nekton, which consists of large animals that may be able to make progress against currents. This scheme includes such species as the animals attached to sargassum and the goose barnacles attached to floating logs under plankton, which to some persons seems illogical. All pelagic plants belong to the plankton. Lohmann (1911) divided the plankton into megaloplankton, the constituents of which are large enough to be readily seen from the deck of a vessel; and nannoplankton, which includes small organisms 1–20 or even 25μ in length. He also divided phytoplankton into euflagellates and aflagellates. The former make up the bulk of the nannoplankton. Peridinians are abundant near the surface; diatoms reach their maximum at greater depths; and coccolithophorids occur at intermediate depths with diatoms or peridinians. Hjort

(1911) has shown that the plants in the open Atlantic are most abundant between depths of 10 and 50 m., where they average 3,000 individuals per liter, and that coastal waters contain more than the open sea contains. The marine floating algae are mostly brown, with a few green and blue-green representatives. They are characterized by thin shells and by various structures for suspension or flotation. Diatoms are more abundant in muddy water near shore, probably on account of the presence of dissolved silica, which they require for their shells. Lohmann (1911) found that there were about 100 bacteria per cubic centimeter in the



FIG. 69.—A plankton catch from the Gulf of Maine; chiefly Calanus, Euchaeta, Sagitta, Tomopteris, Thysanoessa, and Aglantha; Mar. 24, 1920; 200–0 meters. × 1.5. (*From Bigelow* 1926.)

open ocean and 880 or more in harbors. These produce food but are not able to manufacture new organic matter as green plants do. Murray (1914) believes that there are all types of bacteria (putrefactive, fermentive, ammonifying, nitrogen-fixing, etc.) in the ocean, but Lipman (1922) holds that the presence of nitrifying bacteria is doubtful. Luminescent bacteria are found only in the ocean.

Murray (1897) estimated that 70 per cent of ocean plankton consisted of plants, but in a more recent work Murray and Hjort (1912) state that, in the Atlantic, plants constitute about 56 per cent of the plankton. Lohmann (1911) found that about a tenth of the volume of the nannoplankton was made up of proto-

zoans, the greater part being furnished by plants. Willey (1920) states that there are four general types of plankton: (1) *peridinian*, which is often luminescent and composed chiefly of dinoflagellates of the genus Ceratium; (2) *diatom*, in which Chaetoceras is important; (3) *mixed*, composed of diatoms, peridians, and copepods; and (4) *copepod*, made up largely of crustaceans. Johnstone (1908, pp. 150–156), following Cleve, gives an elaborate classification of Atlantic plankton types, based primarily on the diatoms present, and points out that proximity to shore



FIG. 70.—Phytoplankton dominated by peridians, *Ceratium longipes* and *C tripos*, off Cape Elizabeth, Aug. 14, 1914; × 50. (*Bigelow* 1926.)

and temperature are the chief factors that influence the types in a particular locality. He also states that a comparable unit of ocean usually contains less plankton than one in freshwater. Bigelow (1926) gives an excellent discussion of the types of plankton that occur in the North Atlantic, with illustrations. The rate of multiplication of plankton organisms is relatively rapid, so that, while individually small in size, they together maintain a large total bulk because their rate of "overturn" keeps pace with the continual losses.

Animals of Open Ocean.—The animals that live in the open ocean are diverse and specialized in various ways for pelagic life. The Protozoa are represented chiefly by foraminiferans, radio-

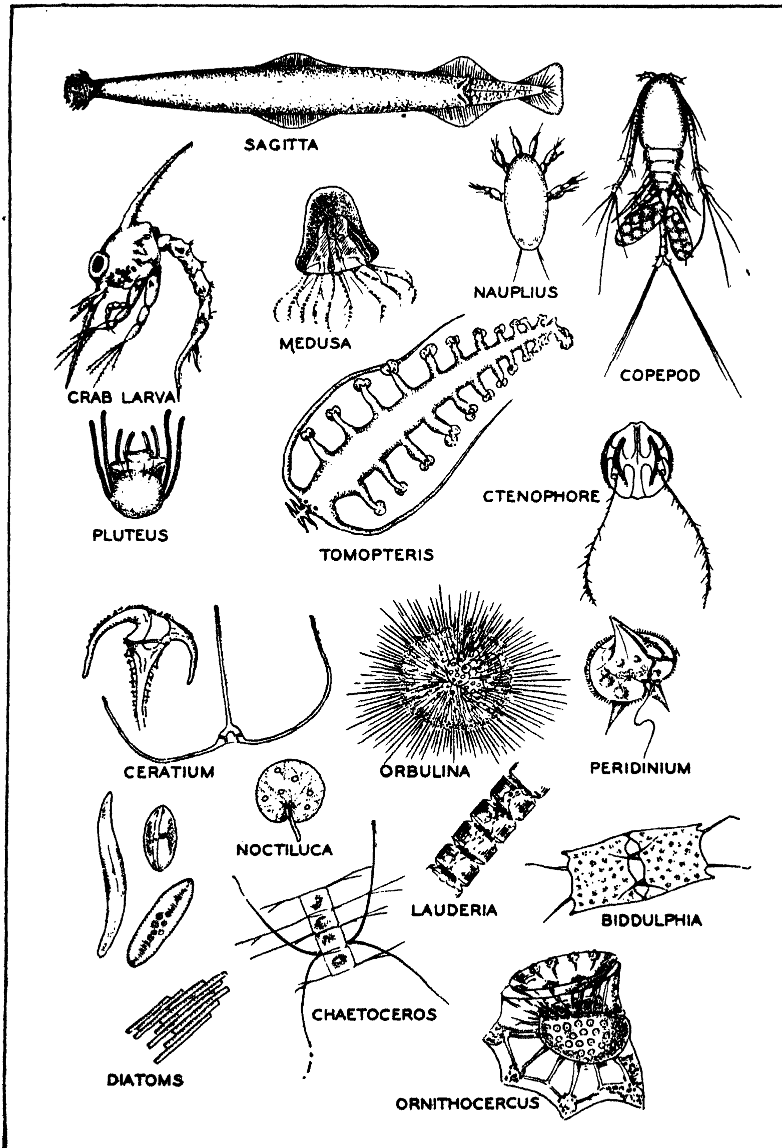


FIG. 71.—Types of plankton organisms, plant and animal; not drawn to same scale.

larians, dinoflagellates (some of which are perhaps to be classified as plants), and tintinnidians. Murray (1895) noted 20 species of foraminiferans from the surface waters of tropical seas. Among prominent metazoans are medusae, siphonophores, ctenophores, copepods, ostracods, schizopods, amphipods, decapods, heteropods, pteropods, cephalopods, tunicates, and fishes. At times the eggs and larvae of fishes and other animals may constitute a considerable part of the plankton. The arrow worms (Chaetognatha) are nearly exclusively pelagic. The nekton includes whales, seals, sea snakes, turtles, sharks, fishes, and other animals.

Origin of Pelagic Animals.—Murray (1895) believes that many pelagic animals arose from the "mud-line animals" of Precambrian seas. He says:

> Whales, seals, pelagic fishes, Halobates, pelagic cephalopods, Ianthina, Scyllacea, pteropods, heteropods, pelagic crustaceans, worms, and coelenterates all appear to bear distinct traces of shore and shallow-water origin.

Brooks (1894) also maintained that all large pelagic animals descended from ancestors that lived near the shore or on the bottom but also held that the pelagic was the first fauna and that bottom animals originally arose from it. The abundance of food at the surface of the open ocean has doubtless been a factor in the spread of such animals as the albatross and petrel. Some animals are found in the pelagic region only at certain stages in their life cycles. The neritic plankton especially is characterized by the presence of the larvae, young, and adult stages of littoral animals. These are often associated with animals that belong in the open sea and have no particular connection with the shore. Murray and Hjort (1912) distinguish between holopelagic animals, which spend their entire lives in the open water, and meropelagic, which pass part of their existence elsewhere. They also point out that the neritic algae of cold seas do not show bipolarity and that those of the open ocean do.

Ranges of Pelagic Animals.—In general, the animals of pelagic regions have wide geographic ranges because there is such a general uniformity in the medium in which they live that there are no real obstacles to spreading. Lohmann (1912) and Ekman

(1935) give valuable accounts of the ranges of distribution of many pelagic organisms.

Effects of Oceanic Currents on Pelagic Life.—The oceanic currents produce marked variations in temperature and to a lesser extent cause differences in salinity. Such differences, when in limited areas, act as barriers for the spread of certain animals. The margins of currents are usually marked on the bottom by the bodies of many dead animals, and certain species, therefore, come there to feed. When there is a radical change in the course of an ocean current there is often a very high mortality among animals both in the new area invaded and in the one that is abandoned. A notable instance of this kind was the destruction of the millions

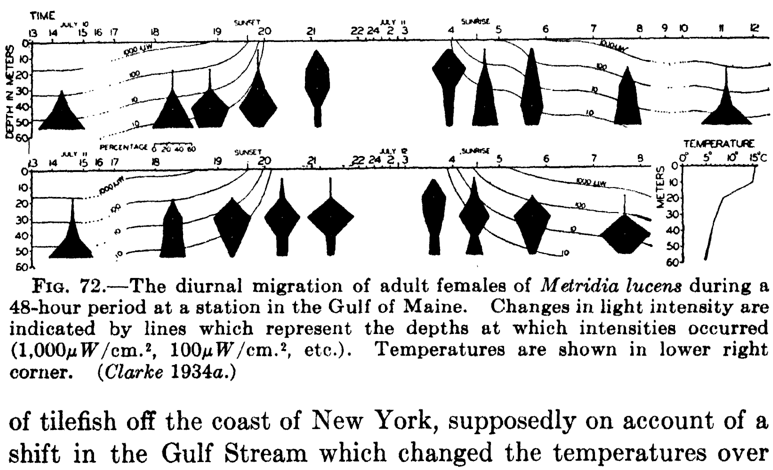


FIG. 72.—The diurnal migration of adult females of *Metridia lucens* during a 48-hour period at a station in the Gulf of Maine. Changes in light intensity are indicated by lines which represent the depths at which intensities occurred (1,000$\mu W/cm.^2$, 100$\mu W/cm.^2$, etc.). Temperatures are shown in lower right corner. (*Clarke* 1934*a*.)

of tilefish off the coast of New York, supposedly on account of a shift in the Gulf Stream which changed the temperatures over banks that were usually covered by warm water. The Gulf Stream reaches its maximum volume in November and dwindles to a minimum in March, each year passing through periodic changes (Johnstone 1908).

Vertical Migrations of Pelagic Animals.—Animals living in the upper strata of the ocean are subjected to annual monthly and daily cycles of changes, and many of them respond by making periodic migrations. There are fishes and other pelagic animals that move to and from particular breeding and feeding areas or strata. Some occupy different areas in youth from those to which they resort during maturity. Of all such movements perhaps the most striking is the general migration of plankton animals toward the surface at night and downward during the day.

The different species of plankton animals maintain a certain separateness and stratification, but many species move upward, in some cases to the surface and in others simply to a higher stratum, for various distances, which usually range from 30 to 50 m. Bourie (1912) says that some fishes come near the surface at night from a depth of 1,000 m. Such species have eyes that are adjusted to light of low intensity. Steuer (1910), in discussing the causes of the daily vertical migrations that are so characteristic of pelagic animals, states that changes in light, temperature, responses to gravity, and the chemical nature of the water all play a part. Light is, of course, the factor that varies most during each day through a considerable stratum of water at the surface, and it is known to be of importance in the migrations of a number of species. In the Gulf of Maine, Clarke (1933, 1934) studied three species of copepods: *Centropages typicus* inhabited the stratum above the thermocline (10–20 m.); *Calanus finmarchius* was irregularly distributed; and *Metridia lucens* occurred below the thermocline. In each case individuals in the upper part of the range were found to have an average length that was slightly less than that of those at deeper levels. The adult females of Metridia exhibited the most marked diurnal migration, the level of maximum abundance rising in the afternoon and during the night and falling in the morning. The movements were found to coincide to a considerable extent with changes in submarine irradiation; *i.e.* the copepods tended to remain in a certain optimum light intensity. Clarke concludes that light is the most important factor in controlling diurnal migration. Ditlevsen (1923) tested plankton animals in an aquarium. He found that they went from areas where light intensity was high into those where it was low and that they spread out in the latter. Eyden (1923) maintains that the specific gravity of animals undergoes periodic changes and that these are the primary factors concerned in vertical migrations. Ritter and Davis (1903) found that Tornaria larvae made daily migrations toward and away from the surface and that they were little influenced by light but responded to changes in the viscosity of the surrounding medium.

Adaptations of Pelagic Animals.—Plankton animals, though derived from diverse groups, show a certain unity in the general nature of their adaptations to pelagic life. They are usually of small size and are thus in close contact with the surrounding ocean

which varies little, thermally or chemically, and resembles the fluids in their bodies. Their specific gravity is near to that of the surrounding water. Weight is kept at a minimum by thin shells; heavier substances are buoyed up by bubbles of gas or drops of oil; sinking is impeded by horizontally disposed spines, bristles, or threads; the body may sink slowly because it is helmet- or parachute-shaped; small animals may adhere in masses which do not sink readily. The eggs of some copepods have egg cases especially adapted to float (Johnson 1934). Some pelagic animals, like medusae, are gelatinous and watery, being really

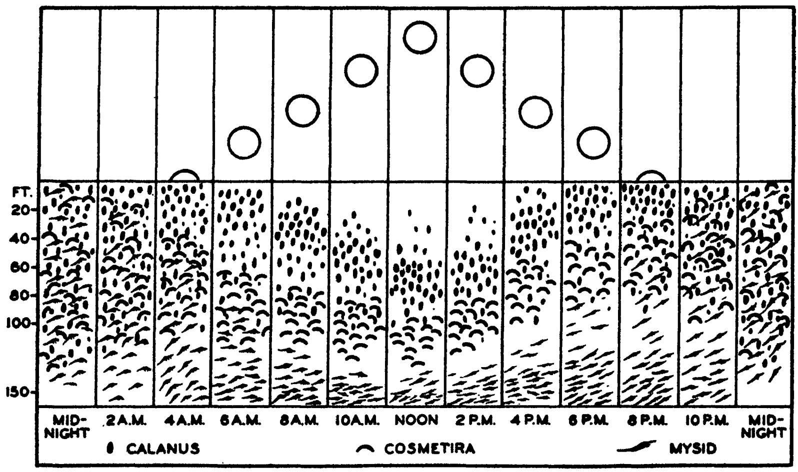


FIG. 73.—Diagram to show vertical migrations of three plankters off the English coast. (*After Russell & Yonge* 1936.)

composed of a mixture of substances that have about the same density as sea water. Plankton animals, as a rule, are feeble swimmers, if they are able to swim at all. Often their peculiar shape makes it easy for them to move toward the surface and at the same time renders sinking difficult. In general, pelagic animals are rather simple in structure—life is easy and the environment is uniform. In depths above 500 m., luminescence is quite characteristic, particularly among fishes. There are some luminescent invertebrates at greater depths. In the "twilight zone," where light is dim but not wholly absent, certain fishes and decapod crustaceans have large eyes and luminescent organs. Fishes that live in depths above 500 m. often have their eyes directed upward. Those living near the surface have rods

and cones in the retinas of their eyes; but those at greater depths have only rods and in this resemble certain nocturnal animals that live on land. The amount of pigment in pelagic animals, in general, increases with depth. Surface species are often transparent; those in the twilight zone, silvery; and those in deeper strata, heavily pigmented.

Nekton.—Many of the larger animals of the open ocean are gregarious (flying fishes, whales, dolphins, birds, etc.), though there are some exceptions. Flying fishes are admirably suited to life on the open sea; and though about 65 species are known, the group shows considerable uniformity in adaptation. The length of these fishes varies from 8–18 in. Swimming in schools, they feed on a variety of foods and are always ready to rise from the surface to escape from predaceous enemies. Whales are also adapted to a striking degree for life in the open sea. They lack hair; have the openings for the nostrils far back; have a heavy blanket of fat beneath the skin; their hind limbs are degenerate, and the front limbs form flippers; the body has a fishlike form. Some sea birds are not only expert swimmers and divers but also have remarkable powers of flight and can endure hunger for long periods. An albatross can live for 35 days without food (Gurney 1899).

Food in Pelagic Province.—The food resources of the ocean depend on light for photosynthesis, which, of course, is limited to a stratum near the surface; and on nitrogenous compounds, which are more abundant near the shore and the surface. Herdman (1909) affirms that, from an economic point of view, diatoms and copepods are the most important constituents of the plankton. Warming (1909) says:

> It is of no slight interest to note that it is not, as in the land flora, starch, with its greater specific gravity, but oil which is the main product of assimilation in the floating plankton community.

Willey (1920) estimates the nutritive value of one copepod as equal to 125 peridinians, or 2,500 diatoms, and points out that a newly hatched smelt has thirty times the volume of a copepod. Pütter (1907, 1923, 1924) has maintained that, because the plankton apparently does not supply enough food to maintain the growth of pelagic animals and because sea water does contain considerable amounts of dissolved nitrogenous substances,

marine animals must obtain nourishment from solutions in the water. Murray and Hjort (1912) and Esterly (1916), who have recently reviewed the evidence for this view, believe that there is not yet enough to support it. Tintinnidians, radiolarians, pteropods, many species of copepods, Dolidium, and salpas feed largely or exclusively on nannoplankton (Lohmann 1911). Some of these animals have wonderful straining mechanisms, capable of removing the smallest organisms from the water. Salpas, appendicularians, and copepods feed on algae. Pelagic protozoans require an amount of food equal to half their own volume daily, and copepods need about one-tenth (Murray & Hjort 1912). Certain copepods feed by drawing into their mouths a vortex containing diatoms and nannoplankton (Esterly 1916, Clarke & Gellis 1935). When kept in membrane-filtered water copepods soon die, but in paper-filtered water they continue to live and grow. This indicates that they use bacteria and other nannoplankters as food (Clark & Gellis 1935). Near Plymouth, England, the spring growth of diatoms is limited by "the grazing of herbivorous plankton animals" (Harvey, Cooper, Lebour, & Russell 1935). Ctenophores are a considerable factor in the destruction of oyster larvae (Nelson 1923). Mayer (1918) reported that the largest jellyfishes were found in cold seas, where food was most abundant, and he noted various species as feeding upon other medusae and fish eggs. Lebour (1923) has investigated the food and feeding habits of several plankton animals. She finds that medusae commonly eat small fishes, which they sting with their trailing tentacles and slowly draw toward the mouth. She also notes that other medusae prey upon crustaceans and that fishes are eaten by Pleurobrachia, Sagitta, and Tomopteris. Willey (1920) reviews the work on the food of herring at Kiel and states that each of 240,000 captured daily for three weeks contained an average of 10,000 copepods. Flying fishes feed on crustaceans, molluscs, and fishes and are, in turn, devoured by dolphins, whales, sharks, bonitos, tunnies, albicores, etc. (Gill 1905). Sea snakes are said to capture food by resting immobile at the surface until little fishes, which are accustomed to gather under floating objects for protection, swim under them; then by a sudden lunge a fish is captured (Klauber 1935). The finback and humpback whales commonly feed on crustaceans (the latter also eating herring and other fishes); while the killer

and sperm whales hunt fishes and larger animals. Penguins, gannets, and other divers prey on crustaceans and fishes. The pelagic birds, like albatrosses and petrels, are in part scavengers and in part most expert fishers. With diatoms and peridinians at one end there is often a long series of steps through various predators to great end products like whales.

Numbers and Rates of Increase of Pelagic Animals.—The pelagic province teems with life, especially near the surface. Johnstone (1908) estimates that there are 457 diatoms and three peridians per cubic centimeter, one copepod per cubic inch, and (by number of the eggs present) a total of 44,172,000 adult female cod in the North Sea. The productivity of most pelagic animals is great, and among species of small size the rate of reproduction is rapid. Murray and Hjort (1912) state that the rate of overturn is more rapid for plants than for animals and affirm that the phytoplankton if unchecked would increase 30 per cent daily. In the South Atlantic, Hart (1934) found four types of diatoms: spring forms, those with spring maxima but persisting at all seasons, those with spring and autumn maxima, and a few with autumn maxima. The time of the main diatom increase falls progressively later in the year toward the poles, and at any latitude the seasonal maxima of different species come at different times. Off California the appendicularians are abundant from October to April but very scarce in summer (Essenberg 1922). Perennial animals spawn at particular seasons, usually once a year; but if conditions are favorable, the productive periods of many invertebrates (amphipods, molluscs) may be prolonged. The production of eggs that float at or near the surface is common among many of the pelagic fishes and other animals. Crustacean, coelenterate, echinoderm, and mollusc larvae also often form a considerable part of the plankton, particularly near shore. Certain flying fishes frequenting the Sargasso Sea deposit their eggs in spheroidal masses inclosed in seaweed.

Zones in Pelagic Province.—The organisms of the open ocean are arranged in zones that show similar relations to depth and latitude, some of the species that occur in cool water at great depths in the tropics being found in shallow water near the poles. Though pelagic species in general have wide ranges, Dahl (1896, 1898) has emphasized the fact that many have very

limited areas of distribution and appear only in certain localities. Temperature is a potent factor in the limitation of horizontal and vertical zones. Murray and Hjort (1912) divide pelagic organisms into four groups: (1) tropical, (2) subtropical, (3) boreal, and (4) arctic and antarctic. In northern pelagic regions plankton organisms attain their maxima below 2°C.; in the boreal, between 4 and 6°C. In the South Atlantic Hart (1934) recognizes four zones for surface waters (0–100 m.): (1) antarctic, (2) subantarctic, (3) subtropic, and (4) tropic. The border of the ice forms the limit of the arctic pelagic region. In the tropics there are more species of plankton organisms but fewer individuals. Organisms secreting lime are more abundant in warm oceans. For example, pteropods in the tropics commonly have heavy calcareous shells but toward the poles are naked or thin-shelled. The tropical ocean also contains many of what Murray (1895) calls "overgrown and more or less paedogenetic larvae," whereas there are few larvae in the cold pelagic regions. The quantities of macroplankton in the uppermost layers of the Caribbean Sea are greater than in the Gulf of Panama, but the volumes for deeper strata are many times greater in the Gulf of Panama (Jespersen 1935). Murray and Hjort (1912) say:

> It has been proposed to arrange the pelagic fauna in certain bathymetrical zones, distinguishing between those forms living in profuse light, or in the region of twilight, or in the dark abyssal waters, but such distinctions are arbitrary, because our knowledge of the bathymetrical distribution of animals is limited, because the laws of distribution are imperfectly understood (for instance, the effects of light), and because the bathymetrical occurrence of certain species is subject to great variation in different regions. We shall therefore dispense with many Latin and Greek terms employed to describe such groups of pelagic organisms, and simply use the term "bathypelagic" to denote those animals that live in the intermediate layers.

While the present writer recognizes the difficulties, he feels that progress will be made if definite formations, associations, and societies are established in the pelagic region, even though it may be necessary with more knowledge to change such groups radically.

Steuer (1910) tabulates the temperatures for various depths at three typical localities in different latitudes, and his figures are

quoted in Table 3. There is a gradual decrease from the surface to the bottom in tropical and temperate regions, but in cold seas the highest temperatures may be in intermediate strata.

TABLE 3.—OCEAN TEMPERATURES IN DEGREES CENTIGRADE

Depth in meters	Cocos Islands	Cape of Good Hope	Antarctic
0	27.4	15.6	−1.0
50	27.1	....	−1.4
100	25.1	14.6	−1.1
200	20.8	....	1.4
300	13.2	....	1.7
500	9.2	9.5	
1000	5.5	4.6	1.6
1500	3.3	2.7	1.6
2000	....	....	0.6
4170	....	0.7	
4600	....	....	−0.5
5834	1.3		

The thermal stratification and the limitation of the penetration of light downward are chiefly responsible for the distribution of oceanic animals in more or less definite strata. In discussing the distribution of the solitary and aggregate forms of Salpa near San Diego, Michael (1918) said:

Solitary forms show an increasing preference, so to speak, as the temperature of the surface water increases from 16 to 20°C.; while aggregate forms show a similar preference as the temperature decreases. . . . Contrary to the prevailing plankton concept, *Salpa democratica*, a typical plankton organism, controls to a significant extent its own distribution just as certainly as does any fish or other animal commonly included in the term "nekton."

At three localities in the North Atlantic, Clarke (1936) found that diatoms were able to carry on a measurable amount of photosynthesis at various depths, according to the penetration of light, as follows: Woods Hole, 18 m.; Gulf of Maine, 40 m.; Sargasso Sea, 140 m. Of course, other factors besides temperature and light vary at different depths. Off the coast of England, Atkins (1922) has found a decrease of pH 0.03 from the surface to a depth of 70 m. From studies along the coast of Washington Shelford (1935) concluded that general hydrographic conditions

(submarine climate) were more important than bottom materials in determining the character of benthic communities.

FORMATION 1. SHOREWATER

The shorewater differs from water in the open ocean in that it is more variable in temperature and salinity; it contains relatively more of suspended and dissolved mineral and organic materials, among which silica and nitrogenous compounds are important. There is a greater variety and quantity of life in neritic than in proper pelagic formations. The characteristic plankton plants are diatoms, which are dependent on silica for the formation of their shells and hence flourish near shore where the supply is most abundant.

ASSOCIATION *a*. ABOVE DEPTHS OF 150 M.

The shallow waters alongshore are subject to the action of sunlight, tidal currents, seasonal changes in temperature, and reduction in salinity by rains and rivers. The flora and the fauna are varied and abundant. A considerable part of the life consists of the adult, young, and eggs of shore organisms, which at certain periods in their life histories have free-swimming stages.

Fasciation 1. Plankton Organisms or Those Attached to Floating Objects.—The plankton of shorewaters often contains considerable numbers of larvae of sponges, echinoderms, annelids, molluscs, crustaceans, and chordates as well as the medusae and larvae of hydroids and certain other adult animals. Such meroneritic representatives of shore animals are associated with holoneritic types such as chaetognaths and copepods. A number of neritic plankton organisms are luminescent. Murray and Hjort (1912) say:

> The peculiar agreement between size, form, and distribution of species and the occurrence of a certain specific gravity and viscosity of the water seems entirely absent in coast waters, where the specific gravity of the water is lower than in the ocean because the inflow of fresh water from continental rivers lowers the salinity. The viscosity, mainly dependent on temperature, should, as a rule, be similar to that of the open ocean outside. We would, therefore, expect to find, for instance, on the coast banks of Africa, similar oceanic forms, or the same faunistic characters on the whole, as in the Atlantic Ocean. On the contrary, we find that the fauna as well as the flora have entirely different features.

For unicellular plants as well as for animals, the rule holds good that all forms are much larger than those of the open ocean. Among plants the minute Coccolithophoridae are replaced by Peridineae; instead of the minute Scopelidae we meet with pelagic herrings and mackerels, animals of quite another size and character.

Schaeffer (1924) states that "the surface water of the Gulf Stream in the Tortugas region contains about 4.56 amebas per 10,000 cubic centimeters of water."

Fasciation 2. Nekton Animals.—There are swimming animals that frequent the shallow waters alongshore. Among these are certain fishes, like the herrings and mackerels mentioned in the last paragraph, seals, whales, gulls, terns, sharks, annelids. Some of these animals live in a variety of situations, like the sharks which range through many shore habitats and with their keen scent seek food on the bottom or near the surface; others, like the mackerels, are characteristic of the open shorewater. Hake when young live as pelagic animals but as they grow older gradually migrate to greater depths (Belloc 1930).

Association *b*. Between Depths of 150 and 500 M.

Wave movements extend to a depth of about 500 meters, where the bottom is marked by the edge of the continental shelf and the soft muddy deposits of deep ocean begin. In depths below 150 m. the amount of light in shorewaters is greatly decreased. Thus there is a "twilight zone" formed between the bottom above 500 m. and the warm surface stratum down to 150 m. In the water in this zone live certain animals that are characteristic.

Fasciation 1. Plankton Organisms.—The plankton below 150 m. is not so abundant as that in the zone above, doubtless on account of the smaller amount of light, but many neritic species are regularly found below the surface stratum. Some of the plankton organisms migrate to or toward the surface at night, and some do not. Esterly (1914) says:

If the behavior of the ctenophore *Pleurobrachia bachei* is compared with that of the chaetognath *Sagitta bipunctata* or of the copepod *Calanus finmarchicus*, the most striking difference is in the exceeding rarity of the ctenophore in subsurface hauls. The chaetognath named and the copepods in general appear to have well-defined levels below the surface

(centers of migration), at which they are more abundant than at the surface, at certain times, and from which they move to or toward the surface at regular intervals during the twenty-four hours. There is no evidence at hand that ctenophores perform these depth migrations.

In a later paper Esterly (1914) also says:

The center of the subsurface region where *Euphausia* is more abundant by day, as shown by winter hauls, appears to be at 300 meters, while *Nyctiphanes* seem to center at 150 meters during the day.

Fasciation 2. Nekton Animals.—Like the plankton many nekton organisms migrate toward the surface at night. Murray and Hjort (1912) say:

Recently it has proved possible to trawl successfully for herring along the sea bottom, but only during the daytime. All sailors can tell us that at night numbers of animals gather in the surface waters, which are never seen there in the daytime. While fishing with long lines on the Faroe banks our lines were set for cod along the bottom in about 200 fathoms; the lines were hauled at night and the stomachs of the cod contained squids, which had been eaten during the day, while at night numerous squids were seen at the surface darting into the glare of our electric lamp hanging over the side.

FORMATION 2. OCEANIC ORGANISMS

The pelagic flora and fauna consist in part of the same species that occur in the neritic biota, but there are also true open-sea species. There are relatively fewer spore-forming species of plants, and peridinians in part replace diatoms. The free-swimming larvae of shore animals are, of course, largely or entirely absent. Oceanic animals do not produce swimming larvae to such an extent as those alongshore.

ASSOCIATION *a*. PELAGIC ORGANISMS ABOVE DEPTHS OF 150 M.

A clearly defined surface stratum in the open ocean is largely confined to a belt that extends on each side of the equator and is poorly defined or absent in cold seas. In this association are certain peculiar resident animals, such as pteropods with heavy calcareous shells, and temporary residents, such as the young stages of fishes which as adults live at deeper levels.

Fasciation 1. Plankton Organisms.—The plankton organisms of the open ocean are typically blue, green, or transparent. Even the blood of young eels is colorless. Haecker (1908) arranged

pelagic radiolarians into four zones: (1) an upper Acanthometra layer; (2) a Challengeria layer, 50 to 400 m.; (3) a Pandora layer, 400 to 1,000 m.; and (4) an abyssal layer. Those in the first group have skeletons of acanthin and are characteristic of warm oceans; those in the others have siliceous skeletons and are usually found in cold water. Among characteristic animals in this fasciation are siphonophores; ctenophores; certain copepods "with wonderful feather or fan-shaped attachments which greatly enlarge the surface of the animals and facilitate their floating"; ostracods; amphipods; pteropods; salpas; and appendicularians. The greatest quantity of life is usually not at the surface but at a depth of about 50 m.

Fasciation 2. Nekton Animals.—Many of the nekton animals of the surface layer, like their smaller and feebler associates, are often transparent, silvery green, or blue. Swimming fishes are perhaps as widely distributed and as representative as any animals in this stratum. True pelagic birds, like the albatross, do not usually go near land except to breed. Whales are confined to the upper layer of the ocean, none of them being able to dive deeper than 100 m. or remain under water longer than about 20 minutes (Parker 1922).

ASSOCIATION *b*. ORGANISMS LIVING BETWEEN DEPTHS OF 150 AND 1,500 M.

This region is the "twilight zone" of the open ocean, where there are unusual specializations for light production and extravagantly developed eyes. With some exceptions luminescence and the size of eyes among decapod crustaceans and vertebrates reach their greatest development at about 500 m. Up to depths of 300 m. the laterally compressed Sternoptychidae with silvery sides and brownish backs are characteristic fishes, but below 500 m. the fishes are usually black and the crustaceans red. "The occurrence of dark colors coincides with the region where the intensity of sunlight is greatly diminished" (Murray & Hjort 1912).

Fasciation 1. Plankton Organisms.—There are a number of plankton animals that in their distribution are rather definitely limited to the twilight zone. Among the radiolarians *Aulographis pandora* ranges from 400 to 1,000 m.

. . . and is considered specially characteristic of these depths. The Tuscaroridae are genuine deep-sea forms, having a bottle-shaped shell provided with large strong spikes arranged in rings around the main axis. In hauls with closing nets they have never been taken in less than 400 meters of water; some species, for instance *Tuscaretta tubulosa*, occur in all oceans.

Sometimes more species of copepods are to be found in the twilight zone than near the surface. The gigantic-eyed amphipod, *Cytosoma neptuni*, occurs at depths exceeding 500 m. Three species of pteropods have been found only between depths of 500 and 1,500 m. (*Peraclis diversa, Limacina helicoides, Clio falcata*).

Fasciation 2. Nekton Animals.—Many nekton animals that are characteristic of the surface do not invade the twilight zones (whales, flying fishes, etc.). There are, on the other hand, a number of fishes that never enter the surface fasciation, though some of the black species from the twilight zone move to the surface at night. Murray and Hjort (1912) captured 286 individuals of the peculiar fish, *Argyropelecus hemigymnus*. They say:

The bulk occurred at depths between 150 and 500 meters; no individuals were caught above 150 meters, and only about 7 per cent were taken at depths lower than 500 meters. . . . It seems, accordingly, that a preponderating majority of the individuals of this species are very strictly limited to an intermediate layer situated at a depth of about 300 meters. A close investigation showed that the individuals captured at 150 meters were all caught at night.

Again, in speaking of their work off the Azores, Murray and Hjort remark:

These catches may be classified into three main regions: (1) a region extending downward from about 500 meters characterized by the occurrence of *Cyclothone* and various black or dark-colored fishes, and of many peculiar invertebrates, red prawns being prominent; (2) a region ranging between 150 and 1500 meters, characterized by a peculiar community of silvery or grayish fishes, belonging to the families Sternoptychidae and Stomiatidae; and (3) the surface region comprising the upper 150 meters, characterized by transparent or blue-colored animals and juvenile forms, especially the members of the large family Scopelidae.

Association *c*. Pelagic Organisms Living below Depths of 1,500 M.

Below depths of 1,500 m. animals are wholly dependent for food on the fasciations above and therefore devour plankton that settles down or feed upon other bathypelagic animals. There is a progressive decrease in the number of animals present at increasing depths. Murray and Hjort (1912) combine all the strata below 500 m. into a single bathypelagic region, and there is much in favor of their point of view. Many of the species that range below 1,500 m. are also found above it; the typically black fishes and red crustaceans begin at 500 m. The fauna of the present writer's bathypelagic stratum consists mostly of types of animals that range from 500 m. to depths greater than 1,500 m., but it seems reasonable to separate those that are able to live in the aphotic zone. The temperature of the ocean below 1,500 m. is practically uniform to the greatest depths. The young stages of many bathypelagic animals are often found at higher levels.

Fasciation 1. Plankton Organisms.—Foraminifera are most abundant in the surface waters of the tropics and decrease with depth or toward the poles, but a number of species of radiolarians extend to the deepest parts of the ocean. In regard to the latter Murray and Hjort (1912) say:

> They occur in all oceans, but sometimes their distribution is very peculiar, for some species live only in abyssal depths under the equator, others at both poles, others only in Antarctic waters; some species live in the surface waters, others between 50 and 400 meters, others between 400 and 1000 meters, others again between 1500 and 5000 meters.

Some range from the surface to depths of 5,000 m. The Tuscaroridae and large Challengeridae are particularly characteristic of the deep sea. Copepods and ostracods occur in the bathypelagic zone. The *Challenger* collected 52 species of ostracods below 500 fathoms, 19 below 1,500 fathoms, and 8 below 2,000 fathoms. Many of these were doubtless associated with the bottom and do not represent true pelagic types. This is true of many animals that have been collected from great depths, and the plankton of the deep sea is, therefore, less well known than that of any other region. The *Challenger* collected species of schizopods at various depths as follows: 32–300 fathoms, 6; 300

to 1,000 fathoms, 4; 1,000–2,000 fathoms, 11; below 2,000 fathoms, 4.

Fasciation 2. Nekton Animals.—Hjort (Murray & Hjort 1912) states that the commonest fishes in the deep pelagic regions are two species of the genus Cyclothone. He says:

> We get the result that there were nine times more individuals in the intermediate layer from 1350 meters up to 450 meters than below 1500 meters. . . . It may be that there is a layer at the lowest depths where there are no individuals and I, for my part at any rate, cannot help believing that the profoundest deep is far more poorly supplied than the intermediate layer.

Hjort also says:

> The smaller and younger individuals live . . . higher up in the water layers than the majority of the largest and oldest individuals. . . . Notostomus and several fishes and squids have been taken only in the deepest hauls at 1500 or 2000 meters.

PROVINCE C. BOTTOM ORGANISMS

The animals that live on the bottom of the ocean beyond the littoral province and below the photic zone have a remarkably stable environment. They live on or in soft ooze, in cold water and darkness, beyond the limits of the action of waves or shore currents. At great depths the pressure becomes enormous. There is relatively more carbon dioxide and less available lime as depth increases, but there is sufficient oxygen to

TABLE 4.—AREA OR SEA BOTTOM OF VARIOUS DEPTHS

Depth, fathoms	Estimated area, English square miles	Percentage of ocean floor
0–1,000	22,000,000	16
1,000–2,000	27,000,000	19
2,000–3,000	81,000,000	58
3,000–4,000	9,800,000	7
4,000–5,000	195,000	
Over 5,000	5,000	

support life at all depths, except in peculiar localities like the Black Sea. Depending on the turbidity of the water, there is no light below 500 to 1,500 m. except that from organisms. Bottom

deposits are important in determining the character of the fauna, and in sheltered situations deep-sea communities may reach higher levels. In terrigenous deposits there is quartz, but lime, iron, manganese, magnesia, and the alkalies seem in the past to have accumulated in the ocean at the expense of the land, and heavier materials are characteristic of greater depths. Beyond continental shelves and abrupt shore lines, the bottom of the ocean for the most part has rather gentle slopes (Shepard 1933). Marine beds on continental plateaus extend down to about 200 m. The littoral includes the tidal zone, the laminarian zone down to about 27 m., and the sublittoral from 27 to 92 m. (Launay 1915). In the last are important food fishes, such as cod, plaice, turbot, and sole. Corals are confined to warmer seas and shallow waters, for they will not grow at less than 20°C. and beyond depths of 64 m. for madrepore corals and 120 m. for millipores.

Murray (1914) summarizes the areas of various depths as in Table 4. Eighty-four per cent is deeper than 1,000 fathoms, but only 7 per cent is below 3,000 fathoms. The Arctic Ocean is shallower than the Antarctic and has a different type of bottom ooze. Johnstone (1908, p. 304) quotes the estimates of Murray and Irvine concerning the total areas of various ocean floor deposits as in Table 5.

TABLE 5.—TYPES AND EXTENTS OF MARINE BOTTOM DEPOSITS

Deposits	Area, square miles	Per cent	Mean depth, fathoms	Mean percentage of $CaCO_3$
Terrigenous:				
Coral sands and muds	3,219,800	2	710	86.41
Others	27,899,300	19	1,016	19.20
Oceanic:				
Pteropod ooze	887,100	..	1,118	79.26
Globigerina ooze	47,752,500	34	1,996	64.53
Diatom ooze	10,420,600	7	1,477	22.96
Radiolarian ooze	2,790,400	2	2,894	4.01
Red clay	50,289,600	35	2,727	6.70

Nearly seven-tenths of the ocean bottom is covered with Globigerina ooze or red clay; only about a fifth is covered by terrigenous sediments.

Distribution of Bottom Animals.—Animals are found at all depths and on all types of bottom deposits, though the density of the population decreases progressively at greater depths.

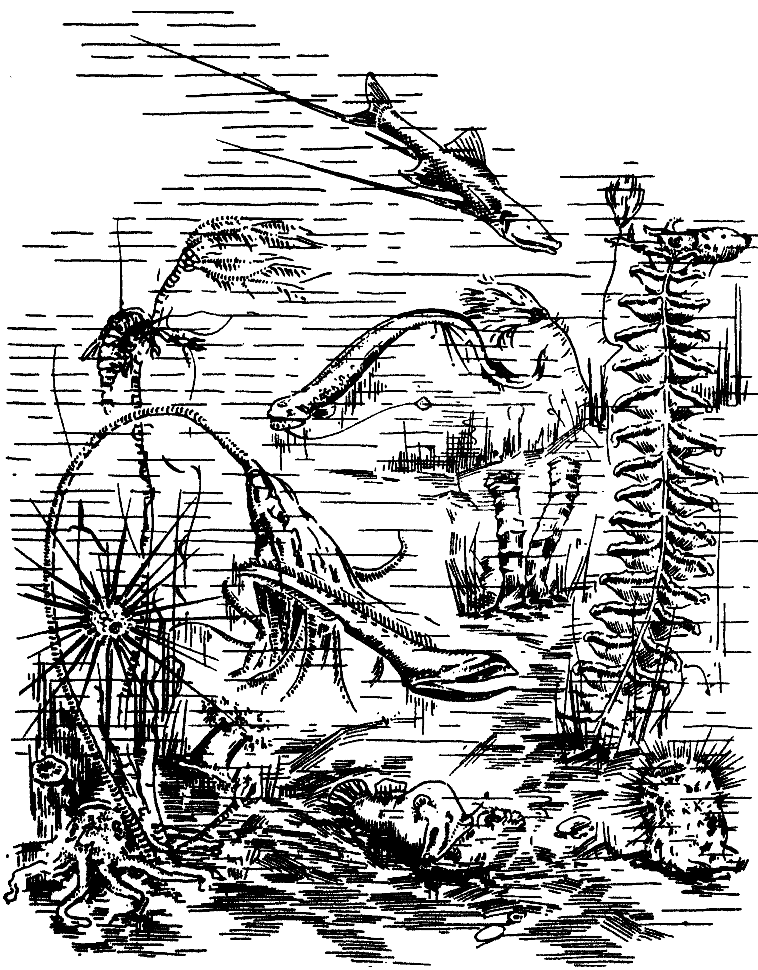


Fig. 74.—Deep-sea animals, from various habitats.

The abyssal plain is scantily populated, and beyond 1,000 fathoms the decrease in numbers is very rapid. Both the pelagic and the demersal regions in the deeper parts of the ocean are rather barren. Johnstone (1908) estimates that for each edible fish

in the North Sea there is an area of about 60 sq. m. and that there are, on average bottoms, about 20 to 200 animals, ranging in size from that of amphipods to fishes, on each square meter. In mussel beds in shallow water as many as 16,000 molluscs per square foot have been found.

Characteristic Bottom Animals in Deep Water.—The fauna of the ooze bottoms does not consist of archaic types but apparently has been for the most part derived from other marine provinces in comparatively recent times. The size of some bottom animals is unusual: Certain crabs spread over an area 3 m. in diameter; pycnogonids attain great size; hydroids grow to a length of 2.5 m.; the isopod Bathynomus reaches a length of 456 mm. Many animals like sponges, coelenterates, crinoids, and ascidians have stalks which enable them to lift their feeding organs above the ooze. There is an ooze-inhabiting medusa that walks over the bottom by means of its tentacles, which serve as stilts and are kept from sinking into the ooze by disks at their tips. This species lacks the marginal sense organs for equilibration that are characteristic of pelagic medusae. The bodies of crustaceans are provided with spines, long antennae, and very long legs, which may be fringed with stiff setae, or spines. Such structures as the last enable crustaceans to walk on the soft mud buttom. Deepwater crustaceans are usually red, but other invertebrates are commonly transparent, blue, or violet. The deepwater fishes beyond the littoral region are, of course, either bathypelagic or demersal. They may be with or without eyes. They are usually slender, black (often even including the mouth, peritoneum, etc.), and have small gill lamellae. Some animals, like barnacles and certain hydroids that depend on hard bottoms, are found at considerable depths in isolated situations if suitable objects for attachment are present. Generally, animals frequenting soft bottoms produce a few large eggs, but a few produce many small eggs.

Some protozoans are truly abysmal. Radiolarians are small with massive skeletons. Among the sponges is none with calcareous spicules at great depths, and even those with siliceous skeletons are not common. Coelenterates are represented by hydroids, anemones, and even corals, which do not form reefs. Sea pens are characteristic forms. Among echinoderms, the crinoids are typical soft-bottom animals. Their stalks may

reach a length of 15–20 m. The echinoids are of interest because those in the deeper parts of the ocean resemble Cretaceous genera and those in shallower waters are related to more modern types. Spatangoids are quite characteristic and often occur in great numbers. The asteroids are much like those in the Littoral Province. Many holothurians are adapted to muddy bottoms; and one group of them, Elasipoda, are abysmal. Worms and wormlike animals are well represented in shallower waters, and a few even occur in red clay at great depths. Phoronis is found at depths between 4 and 200 fathoms. Rhabdopleura, Cephalodiscus, gephyreans, serpulids, and terebellids are soft-bottom forms. Those that occur at great depths, of course, do not secrete lime but live in leathery tubes. The abysmal Errantia are generally eyeless. Brachiopods are not markedly different from littoral types. Molluscs that range to considerable depths have thin shells and lack pigment. Few species of clams or snails are abysmal. The cephalopods that live at great depths are not peculiar. The arthropods are well represented in the abyssal region. There are few entomostracans or amphipods, but some of the latter are totally blind. There are several characteristic isopods, and even some abyssal barnacles. The fishes, though largely teleosts and hence of the most modern types, perhaps show as characteristic modifications for life in the deep sea as any group. The dark hues, attenuated forms, barbels, fin filaments, and large mouths with long irregular teeth make them unique. Anglers are well represented in the bottom fauna, and some species have luminescent lures.

Appellöf, who wrote about bottom animals in Murray and Hjorts' "Depths of the Ocean" (1912), states that demersal shrimps and amphipods creep almost as much as they swim. Currents are important in distributing such animals and the pelagic larvae of others, like those of holothurians, which do not swim at all. Currents also bring food to bottom animals and in places sweep fine deposits away, so that sedentary animals may find firm resting places. The distribution of bottom animals is, of course, "much affected by the character of the sea floor, since whole groups of animals are limited by their structure or mode of living to some particular kind of bottom." This is particularly true of mussels, worms, and echinoderms. Some species of sponges and corals, "belonging to groups most

of whose members are attached and therefore confined to rocky bottom, have developed special organs in the way of root-like outgrowths by means of which they adhere to soft bottom and can therefore rest there normally." Sea pens and crinoids are held above the ooze by their stalks. In the Atlantic most of the bottom animals are associated with the terrigenous deposits and Globigerina ooze, but a few are found on red clay. In their discussion of demersal fishes, Murray and Hjort (1912) state that:

> While the fishes of the continental shelf all live on terrigenous deposits, like blue mud, the "Michael Sars" results prove that, in the Eastern Atlantic at any rate, *most of the fauna of continental slope live on Globigerina ooze.* . . . The results show in any case that the Globigerina ooze in depths of 550 to 1000 fathoms may be a rich ground for animal life. . . . At Station 53 south of the Azores, 2615 to 2865 meters, the trawl captured in one haul, besides 39 fishes, about 500 holothurians, and the animals that are characteristic of calcareous oozes are therefore not identical with those that are found on the siliceous, radiolarian, and diatom oozes of the coldest polar seas.

Limits of Abyssal and Shallow-water Animals.—The upper limit of the abyssal region is not clearly defined. Appellöf (Murray & Hjort 1912) says:

> The upper limit certainly presents great difficulties, but I believe that a great many of the forms which characterize the archibenthal belt [steep continental slopes] do not as a rule extend into depths less than 800 meters, though it is possible that certain forms may be met with at 600 meters. We have not yet acquired sufficient knowledge of the factors regulating vertical distribution to be able to divide the different parts of the Atlantic into vertical zones, and a division of this kind will, I fancy, always be more or less a matter of personal opinion. Besides it is undeniable that forms which properly belong to the abyssal fauna [that on the comparatively level, deep, ocean floor] may find their way to the lower parts of the archibenthal zone, and that archibenthal forms may go down into the abyssal region, while, given favorable conditions, certain littoral and sublittoral forms may descend below the upper limits of the archibenthal belt. In any case there is no clearly defined boundary between the archibenthal and abyssal areas.

The associations and strata that the present writer lists on page 225 are not to be taken as rigid, fixed areas but as overlapping and variable in extent. Notwithstanding this, there are

species that are primarily abyssal, and others that are characteristic of intermediate strata. Murray (1914) places the change to benthos at 400 to 500 fathoms.

Food of Bottom Animals.—Many bottom animals eat ooze or catch falling organisms or organic particles that settle down from above. One species of ooze-eating crustacean has a long, coiled intestine—a rare peculiarity among arthropods (Calman 1911). There is a great feeding ground at the "mud line," just beyond the edge of the continental shelf, where shore currents cease to stir up the sediments. Below depths of 500 (in some cases 1,500) m. there are no plants that carry on photosynthesis,

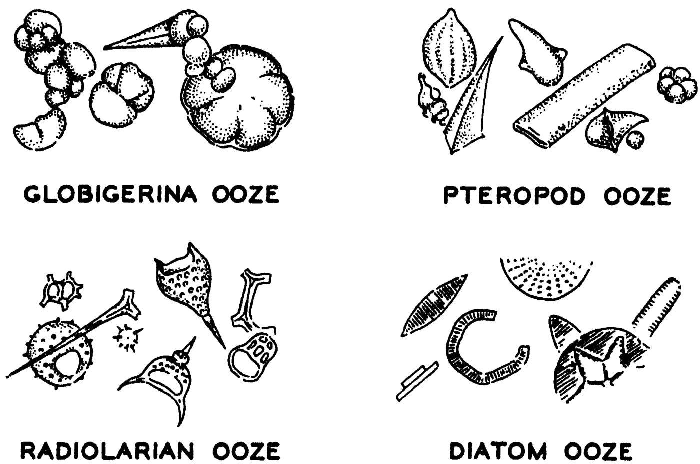


FIG. 75.—Typical ooze animals and diatoms.

and organic food must, therefore, have its origin near the surface. Schizomycetes are prevalent at depths of 800 to 1,100 m. (Warming 1909) and change ammonia into nitrates or nitrites. At great depths little lime is available. The bones of fishes and the shells of molluscs and crustaceans are accordingly lacking in calcareous materials. Clemens (1921) described the food of the muttonfish as consisting of molluscs, echinoderms, and crustaceans. In summer this species feeds in bays and estuaries but from October to May forages over the ocean bottom. In the Kattegat, plaice, during the first months of the bottom stage in their life cycle, eat copepods, amphipods, cladocerans, and ostracods; later they consume chaetopods and lamellibranch larvae; but by September they eat chiefly bottom lamellibranchs

(Blegvad 1930). It is estimated that 229,000 tons of bottom animals are available annually in East Kattegat, and this is sufficient to produce 12,800 tons of plaice (2,600 tons were caught in 1928). Blegvad (1916) has made an extensive study of the food relations of various animals in the ocean near Denmark, and certain of his findings are presented in Fig. 23. Both he and Petersen (1918) emphasize the importance of organic ooze as a source of food for marine animals. Being interested in the productiveness of the ocean, they also point out that small fishes and other animals that are not eaten by man, or his food fishes, are to be classified as injurious because they occupy space and use materials that might otherwise furnish human food.

Zonation of Bottom Animals.—In her report on certain groups of demersal annelids from the Pacific, Essenberg (1918) says:

> The polynoids are divisible into littoral, sublittoral, and abyssal species according to their bathymetrical distribution. . . . The facts that certain species are restricted to definite life zones and to definite ranges of temperatures, that the same species occurring in widely separated areas occur in depths of similar temperatures, and that boreal species occur in temperate and subtropical zones as deep-water species seem to point to the conclusion that temperature is the chief factor in determining distribution. . . . The greatest number of polynoids are found in the littoral zones where food is more abundant. . . . The deep-water species differ considerably from the littoral species, and certain characteristics, such as thin cuticle, the smaller size, the delicate elytra and eyeless condition of many abyssal species point to the conclusion that the latter have undergone a degeneration and physical specialization which make them fit for that particular environment only. . . . The great uniformity of littoral species and the great diversity of abyssal genera and species lead to the conclusion that the littoral zone is the center of origin, or the center of dispersal of polynoids, and that species migrate or are driven to abyssal areas where they undergo great specialization and partial degeneration.

Murray and Hjort (1912), Galtsoff (1924), and others have noted a stratification, which is chiefly dependent on temperature, in the arrangement of demersal fishes. Johnstone (1907) points out that "deep-sea" fishing is largely above the 200-m. line, and Meek (1916) notes that the young of demersal, as well as those of pelagic, fishes commonly occur at higher levels than adults. Though most bottom animals are confined to rather

definite strata, some have wide ranges. Hickson (1894) mentions a pycnogonid that occurs from low-tide mark to a depth of 2,225 fathoms. Shelford (1918) showed that animals brought up from a depth of 2 fathoms were twice or thrice as resistant to lowered salinity and increased temperature as those of the same species from a depth of 75 fathoms, but the latter were more resistant to variations in acidity or alkalinity. On the west coasts of South America and Africa the upwelling of cold currents more or less obliterates stratification, and typically deepwater animals occur at higher levels.

FORMATION 1. BOTTOM ON CONTINENTAL SHELVES

The Norwegian (Murray & Hjort 1912) and Danish (Petersen 1918, Blegvad 1916) biologists have made comprehensive and detailed studies of the life on the sea bottom along their shores, and their writings present the best account of animals and their relations. A continental shelf, of course, offers a variety of environmental conditions and thus differs from the ocean beyond the action of shore currents and light where the bottom and temperature are very uniform. A variety of societies are accordingly present.

Association *a*. Terrigenous Deposits

Petersen (1918) lists, as follows, nine communities that are characteristic of the bottoms on the continental shelf and in littoral regions near Denmark: (1) Macoma or Baltic community, which may be subdivided according to the type of bottom (Mytilus, Mysis, Mya, and Littorina occurring on sand; the plant belt having these types and also an "epifauna" of other species; muddy areas being characterized by eels and polychaetes); (2) Abra community in deeper water, consisting largely of clams and sea urchins that are not eaten by fishes; (3) Venus community on open sandy coasts in depths of 8–38 m.; (4) Echimocardium-Filiformis community at intermediate depths, 38–41 m.; (5) Brissopsis-Chrajei community, in deep parts of the Kattegat up to 700 m.; (6) Brissopsis-Sarsii community, in deep parts of the Skagerak; (7) Amphilepsis-Pecten community, in deepest parts of the Skagerak; (8) Haploops community, on soft clay bottoms where there may be 3,500 worm tubes per square meter;

(9) deep Venus community. It will be seen that Petersen's groups are chiefly characterized by particular clams and worms that are practically nonmotile and therefore serve as good indicators of particular conditions. Thorson's (1934) observations in Scoresby Sound showed three zones: (1) a surface layer only a few meters thick with positive temperatures and low salinities; (2) a layer down to 300–400 m. with negative temperatures (0.0 to −1.69°C.) and salinities of 32.3 to 34.8 ‰; and (3) a layer with positive temperatures (0.0 to 1.50°C.) and constant salinity of 34.69–34.95 ‰. Lamellibranchs dominate in shallower waters; polychaetes, in deeper waters. At a depth of 100 m. the total weight of bottom animals was 50 per cent less than at 10–20 m.

Many littoral animals are distributed over the floor of the ocean far below the strictly littoral strata and these constitute the greater part of the animals on terrigenous deposits.

Fasciation 1. Burrowing and Sessile Animals.—The burrowers in this stratum are mostly clams, sea urchins (particularly the bilateral types), and annelids. The food of these consists chiefly of mud and living or dead plankton. The same is true of the comparatively few animals, such as barnacles and hydroids, that are attached to the hard parts of other animals or to the rather infrequent hard objects, such as sharks' teeth and pebbles, that rest on the bottom.

Fasciation 2. Swimming and Crawling Animals.—Over the surface crawl a few snails and crabs; amphipods swim or crawl about. These feed upon ooze or the larger portions of dead plants or animals. Nautiloids and predaceous fishes like the cod and eel swim about and eat the invertebrates. As in the pelagic region, there is a transition in color and pattern among bottom animals. In littoral habitats occur many colors and patterns, but at greater depths monotones of dull hue prevail. Luminescence also reaches its maximum at a depth of about 300 m. and decreases toward the surface or the abyss.

Association *b*. Calcareous Oozes

Pteropod ooze occurs in depths of less than 3,000 m., and Globigerina ooze ranges from 3,000–5,000 m. Just beyond the edge of the continental shelf, where the slope into deep water begins, is the mud line, at a depth of about 500 m. Here soft

ooze replaces the coarser sediments that are characteristic of shallower water. In this stratum large amounts of organic materials from higher levels accumulate on the bottom, and many animals feed on them. Clark (1908) points out that the largest crinoids occur at depths between 100 and 600 fathoms, where most dead microscopic food falls. Murray (1895) points out that a greater variety of species occurs on terrigenous deposits but that more individuals per unit area may occur along the mud line. Below the mud line at about 3,000 m. the deep-sea deposits begin with Globigerina ooze. Murray states that 2,050 species of animals had been captured between depths of 500 and 3,000 m. up to the year 1895.

The burrowing and sessile animals (Fasciation 1) are similar to those in the zone above, as are their relationships to predaceous species and the scavengers that swim or crawl (Fasciation 2).

FORMATION 2. ABYSSAL

The soft oozes in the deeper parts of the ocean support a considerable variety of animals, but the number per unit of area is always small. Though a number of species have wide ranges, there are also many that are apparently restricted to particular localities. In temperate seas arctic types begin to predominate at depths of about 800–1,000 m., and the abyssal animals are largely cold-water animals. But calcareous deposits do not occur in the coldest seas; and though Globigerina ooze extends to considerable depths, it is replaced by deposits composed chiefly of silica or clay below 5,000 fathoms.

The fauna of this deepest region is still imperfectly known because comparatively few dredge hauls have been made, and in collecting with a dredge there is always some doubt as to whether animals that can swim were actually captured near the bottom or at some intermediate point on the long journey from and to the surface. Such types as worms, molluscs, holothurians, and starfishes are undoubtedly demersal, but the habitats of fishes or crustaceans are often uncertain. Murray and Hjort (1912), however, list 21 species of fishes, collected before their expedition in the *Michael Sars,* that apparently came from the bottom at depths of more than 2,000 fathoms, but these species were represented by only 35 individuals, or an average of somewhat less than two each.

ASSOCIATION *a*. CALCAREOUS OOZES

Many invertebrates frequent calcareous bottoms in the abyssal plain beyond the continental slopes. Apellöf (Murray & Hjort 1912) sets the limits of the archibenthal fauna at about 2,000 m. He found that many of the abyssal species that occurred off the coasts of Africa and Europe were not taken off the American coasts and that common species on the west of the ocean were often absent on the east. He therefore concludes that many of the invertebrates do not have wide geographic ranges, and this was particularly true of those that live on Globigerina ooze. Three bilaterally symmetrical holothurians (*Deima fastosum*, *Peniagone wyvillii*, *Oneirophanta* sp.), a starfish (*Freyella sexradiata*), and a sea urchin (*Salenia hastigera*) are, however, cited by Apellöf as examples of true abyssal species.

The abyssal fauna living on calcareous oozes consists of protozoans, sponges, medusae, anthozoans (the stalked sea pens being characteristic), archaic crinoids and echinoids, peculiar starfishes and holothurians, brachiopods, sipunculids, annelids (some eyeless), molluscs, amphipods, isopods, barnacles, schizopods, decapods, pycnogonids, ascidians, and fishes. The large-eyed, big-mouthed, acuminate-tailed fishes of the genus Macrurus apparently dominate the abyssal plain.

Murray and Hjort say:

If we fix the boundary of the abyssal plain at the 2000-fathom line, we may consider the area between the 2000- and the 1500-fathom lines as an intermediate zone between the abyssal plain and the continental slope. . . . The "Michael Sars" made three hauls with the trawl in such depths, which, compared with our results on the abyssal plain, are very interesting, and invite inspection of their details:

Station 35. South of the Canaries, 1424 fathoms (2603 meters). Trawl dragged two hours. Result of haul: many siliceous sponges (including *Hyalonema*), hundreds of holothurians, large prawns (*Benthesicymus*, n. sp.), 18 bottom fish (9 Macrurids, 1 *Bathysaurus*, 2 *Holosauropsis*, 5 *Alepocephalus*, 1 *Hariotta*).

Station 53. South of the Azores, 1430 to 1570 fathoms (2615 to 2865 meters). Trawl dragged three or four hours. Result of haul: 2 large and many small sponges, 3 mussels, 5 cirripeds (*Scalpellum*), 30 large prawns (*Aristeopsis*), 15 hermit crabs, 5 *Pentacheles*, 1 large white decapod (*Mundopsis*, n. sp.), 500 holothurians, 39 bottom fishes

(17 *Macrurus*, 5 *Halosauropsis*, 2 *Benthosaurus*, 2 *Bathysaurus*, 2 *Bathypterosis*, 6 *Alepocephalus*, 5 *Synaphobranchus*).

Station 88. North of the Azores, 1700 fathoms (3120 meters). Result of haul: a great number of holothurians, sea urchins, starfish, ophiuroids, some crustaceans (*Polycheles*, *Munidopsis*, *Parapagurus*), 21 bottom fishes (17 *Macrurus*, 1 *Bathysaurus*, 3 *Histiobranchus*).

We thus see that *it is not terrigenous deposits alone which harbor an abundant bottom fauna;* in fact, on true pelagic deposits, like Globigerina ooze, we may have the conditions necessary for abundant life.

The suitability of a deposit does not depend on the amount of calcium present, but "the important item is the *organic substance* contained in the deposits, which fertilizes the surface layers."

Associations *b*, *c*. Siliceous Oozes and Red Clays

These associations are apparently not unlike those that occur on calcareous oozes. They are, of course, characteristic of deep and cold oceans and are not so well known as those in regions that are more densely populated and readily accessible.

CHAPTER IX

FRESHWATER

Characters of Freshwater Habitats.—The total area of freshwater habitats on the earth is very small compared with that of the ocean or land. Animals living in lakes, ponds, streams, pools, or swamps are, accordingly, more isolated and hence often have less chance to avoid unfavorable conditions by migrating. The salt content and the osmotic pressure in freshwater are variable and, of course, much less than those of the ocean. The amount of salts averages about 0.18 per cent. In rain water there are 30–40 parts of solutes per million; drainage water contains 50–230; springs, 60–350; rivers, 120–350; ocean, 33,000–37,370. Ocean salt is made up largely of sodium chloride while the salts in freshwater are mostly carbonates. Freshwater is much more variable than the ocean, and its inhabitants are, therefore, generally subject to greater fluctuations in temperature, dissolved gases, turbidity, light, and food. Tides are very feeble or absent, and currents are, therefore, more important because they tend to overcome thermal stratification and the variation in gases that is associated with it. All bodies of water that are in contact with the atmosphere carry on a respiratory exchange with it, and the amount and nature of the gases exchanged vary with annual cycles and other fluctuating conditions. Ground waters are usually favorable for the growth of diatoms because they contain much carbon dioxide. The presence or absence of carbon dioxide also affects the reaction and concentration of ions. The clearness of water determines the depth to which light can penetrate and at which photosynthesis can take place. Conditions for penetration will, of course, be better in a clear lake than in a turbid stream. Water of precipitation is clear and in a sense reasonably pure. It washes minerals and other substances into bodies of freshwater where they are arrested and perhaps appropriated, digested, and assimilated by plants or animals and thus make continual contributions to the life in such situations. The total volume of a body of freshwater and its volume in

relation to its area are important. In a general way the size of animals is related to the extent of the basins that they inhabit. The largest fishes are usually found in the largest streams and lakes. A deep lake with a very limited surface area will show pronounced thermal stratification, but in a shallow lake such a condition is prevented by continual circulation through the action of winds.

Origin of Freshwater Animals.—Evidence from fossils indicates that the animals that lived first on the earth were largely or wholly marine and that land and freshwater habitats have been populated by repeated invasions from the ocean. This view is further supported by the fact that the distribution of certain groups living today is entirely confined to the ocean and by the similarity that the composition of the blood of land and freshwater animals bears to sea water. Probably no great groups of animals have arisen outside the ocean (Hesse 1920, Pearse 1936). However, Barrell (1916) and Romer and Grove (1935) have shown that fishes originated in freshwater. Though it is possible that certain insects invaded land from freshwater, there is no doubt that arthropods had their origin in the ocean, and many insects certainly entered freshwater from land. Pelseneer (1906) has reviewed evidence that indicates that marine animals are at present becoming adjusted to freshwater, especially along the coast of southeastern Asia, where heavy rains considerably dilute the ocean. Animals have apparently taken up life in freshwater by slowly migrating up rivers, by being marooned in bays which were cut off from the sea and in which the water gradually became fresh, and by movements from land habitats. Murray (1895) suggests that freshwater animals have been derived from those of the marine "mud line," because free-swimming larvae are rare in both situations. It is certain that the glaciated regions in the Northern Hemisphere were free from aquatic life and have been repopulated since the ice retreated. The deepwater animals in the lakes in such regions have apparently been derived from the local fauna in each case, and there is no general relationship even between those in various parts of the same continent. The invasion of freshwater habitats apparently has been through spreading and adjustment to local conditions.

Invasion of Freshwater from Sea.—In going from the ocean to freshwater there is a marked change in salinity, and animals

making such a change must be more or less euryhaline. The living membranes of some animals will not permit them to invade freshwater, but other animals (certain species of Fundulus, Sesarma, etc.) can swim directly from the ocean into rivers without apparent injury. Animals of the latter group are able to maintain the liquids within their bodies as they were in the ocean, or the liquids become diluted without injuring them. The body liquids in Fundulus do not change markedly when the minnow invades freshwater, but the salts in the blood of crabs may vary from 1.5–3.5 per cent. Animals that have migrated from the land into freshwater may continue to breathe air and though living "in" water are not really "of" it; others profoundly modify their methods of respiration. Aquatic insects usually breathe through tracheae like their land ancestors, but many, particularly during larval stages, have acquired tracheal or blood gills and respire directly from water. Some aquatic insect larvae can live for months after their blood gills have been removed (Morgan & Wilder 1936). Such organs are apparently not necessary for respiration and probably also serve other functions, especially excretion (Karny 1934). The permeable membranes in freshwater animals have to do much more work to maintain the equilibrium of internal fluids than those of marine animals. Respiration also requires the expenditure of much more energy (Fox & Simmons 1933, Schlieper 1935). In freshwater there is less competition between varied types, and, according to Darwin (1859), new forms are produced and exterminated more slowly. Some types of animals have never been able to establish themselves in freshwater, but species that have done so have, in some cases, been able to persist when their relatives that remained in the ocean became extinct. Hesse (1920) cites the hydra, certain crabs and ganoids, and dipnoans as primitive representatives of groups that have died out completely, except for those that have found a refuge in freshwater habitats.

Freshwater Faunas.—Freshwater faunas are, in general, distinguished by their lack of variety when compared with those of land or sea. No phylum is confined to freshwater; in fact, the only great groups that are so limited are the Amphibia and Dipnoi. Semper (1881) lists many genera, families, and some orders that are restricted to freshwater. Heliozoa, ctenophores, echinoderms, and brachiopods are wholly absent; sponges,

bryozoans, and coelenterates are represented by only a few species. The immature stages of certain insects (damsel- and dragonflies, stoneflies, Mayflies, caddis-flies) are largely or wholly confined to freshwater. These show considerable specialization for various habitats and apparently have long been associated with them. Caddis-fly larvae commonly live in cases, which they attach to objects or carry about according to the swiftness of the currents in the surrounding water. Odonate nymphs have rectal or caudal gills and show a high degree of adjustment to particular habitats—burrowing, clinging to plants, etc. Such types have perhaps been aquatic throughout their phylogenetic development. Water bugs, on the other hand, apparently are recent immigrants into aquatic habitats, for they breathe air and are largely carnivorous.

Adaptations of Freshwater Organisms.—Freshwater plants and animals have certain characteristics that adapt them to the habitats in which they live. The roots of freshwater plants, in general, appear to serve more as holdfasts than extractors of nourishment, though Pond (1905) holds that they may play an important role in imbibition. Water-carrying tubes, mechanical tissues, and secondary growth in thickness are absent or poorly developed; large air spaces and thin epidermis are characteristic, and there is often provision for the excretion of water; stomata are generally absent from submerged parts; chlorophyll is usually near the surface of plants, where it can best receive the comparatively weak light (Warming 1909). Many freshwater plants are perennials, and vegetative propagation by buds, rhizomes, bulbs, and other means is common. Among freshwater animals there is a rather general absence of free-swimming larval stages and a general tendency toward the formation of considerable amounts of yolk in eggs. There is also a prevalence of many types of special adaptations that enable animals to survive desiccation, foul water, extreme temperatures, or other unfavorable environmental fluctuations—the ephippia of cladocerans; the "winter" eggs of cladocerans, rotifers, and rhabdocoels; the gemmules and statoblasts of sponges and bryozoans; the cysts of copepods, annelids, and protozoans. There are also membranes that prevent the excessive absorption of water or the undue loss of salts from the body fluids (Adolph 1925). In many cases there are special structures for the elimination of water—freshwater

protozoans possess contractile vacuoles, which are absent in marine representatives of the same phylum. Hesse (1920) states that a Paramaecium at various temperatures may eliminate from thirty-one to seven hundred times its own weight each 24 hours. Crabs excrete urine more rapidly in freshwater than in the sea (Schlieper 1935). Animals that have recently invaded freshwater from the land or ocean have become adapted in various ways but often show little modification in the patterns of physiological processes or in the structures that functioned in their old habitats. Aquatic insects for the most part breathe air, and their tracheal systems are quite similar in their general plans to those of related terrestrial species. Needham and Williamson (1907) point out that dytiscids are adapted to life in water by (1) great bodily rigidity brought about by fusion and compression of parts; (2) diminished resistance to water by rounding of contours, assumption of boat shape, depression of eyes, loss of hair and sculpture, reversal of antennae, flattening of legs; (3) great swimming efficiency through flattening, developing fringes, loss of claws, etc.; (4) ability to stay under water by provision for the storage of air or ability to exchange gases with the surrounding water. Leng (1913) states that some beetles are able to remain submerged for weeks. Needham (1902) showed that insects have become associated with freshwater habitats in various ways and to varying degrees. Those that breathe air may run over the surface, rest beneath the surface film and remain attached to it, or remain below the surface and secure air by means of a long breathing tube or from the gaseous stores of aquatic plants. Those that breathe from water may be swimmers, climbers, clingers, crawlers, or burrowers. Barber (1913) ascribes the adjustments of water-inhabiting bugs to specializations in locomotion, respiration, methods of feeding, and ability to endure foul water.

Food of Freshwater Animals.—The food relations of freshwater animals are somewhat different from those that obtain in other realms, but there is, of course, the usual dependence on photosynthesis as the basic process for food production. Freshwaters differ from the ocean in their lesser salinity and in the lability of carbonates, which are readily dissolved as bicarbonates when carbon dioxide is present or assume a more stable form in its absence. Some algae are able to take carbon dioxide from bicar-

bonates and thus to carry on photosynthesis. Assimilable nitrogenous compounds are, of course, essential and are supplied by nitrates, nitrites, and ammonium compounds; the activities of bacteria; and organic compounds from other living organisms. The limited size of freshwater habitats and the consequent nearness of all their parts to the seats of photosynthetic activity make it possible for detritus and other organic foods to be distributed readily into their remotest situations. There will ordinarily be more food and more animals on the bottom of the deepest lake than on the barren abyssal floor of the ocean.

Classification of Freshwater Habitats.—Various classifications have been proposed for the group of organisms living in freshwater. Steuer (1910) and Needham and Lloyd (1916) have stressed the differences encountered by the inhabitants of the shore habitats in relation to those of the open water. Embody (1922) and Klugh (1923) emphasized the importance of temperature differences. Shelford (1911), Ward and Whipple (1918), and Klugh (1923) contrast moving with quiet water and intermittent with continual flow. The classification outlined on page 225 seems more natural. Natural groupings appear to be: (1) lotic waters (streams); (2) lentic waters (lakes and ponds); and (3) paludal waters (swamps and pools).

Streams flow, carry considerable suspended matter, and may vary considerably in volume. Swift streams have more or less constant temperatures throughout the year; large, slow streams vary greatly in temperature. Current movements in lakes and ponds are usually slight, but waves may be important in their shallower parts; thermal stratification and its attendant gradient in dissolved gases are frequent. Shallow swamps and pools have little movement, even of waves; height of water and temperature vary greatly in different seasons.

PROVINCE A. LOTIC, OR FLOWING, WATERS

Streams.—"A large lake represents stability of environment, but a flowing stream is the fullest expression of a condition of instability" (Purdy 1923). Streams flow, carry and deposit sediment, and vary greatly in volume. They have been classified as (1) permanent, (2) those that dry up occasionally, and (3) those in which water is present only occasionally (Needham &

Lloyd, 1916), but the writer feels that from a biological point of view streams are more naturally distinguished as swift or sluggish. Streams are not inherently very rich in food resources but compensate for such deficiency by serving as highways for animals which are, through them, able to gain access to habitats where there is much food. The fauna of any stream is, of course, related to the location of its basin and its past history. In New Zealand there were no stream fishes until they were introduced by men. In general, stream animals are assorted according to the volume of water available, the larger animals usually occurring in the larger streams.

Variation in Amount of Water.—The variation in the amount of water passing down a stream has various relations to the animals present. The Illinois River flows 227 miles. At flood water it passes through the entire course in about 5 days but requires 23 days for the journey at lowest water. In this river, rains have been found to bring in decomposable matter and thus decrease the oxygen content of the water. Turbulence and swiftness injure many animals during floods, and some may actually be swept away altogether. The beetles that dwell near the banks of streams go ashore during floods and thus escape. Winds blow rubbish and floating objects against the shore and thus help the insects to reach the land. Beetles of the genus Stenus "skim" during floods by secreting a substance at the posterior end which drives them along the surface by differences in surface tension (Joy 1910). Abbott (1870) found that fishes soon sorted themselves into their accustomed habitats after a freshet, but Shelford (1911*a*) noted that it required about a year for the river snails Pleurocera and Campeloma to move a mile upstream. Droughts cause most fishes to move downstream, but some, like the horned dace, are able to persist in the pools left in intermittent streams. There is a general zonation of animals in streams from source to mouth according to the swiftness, temperature, and volume of water present. Ide (1935) made a careful study of the distribution of May-fly nymphs. He found that the number of species increased downstream but that two headwaters species were absent there, probably on account of high temperatures. Some species were unable to maintain themselves near the source because temperatures were not high enough to permit complete development.

Food in Streams.—The available food in streams comes from (1) the large, aquatic vegetation, of which there is usually little in the actual channels; (2) plankton; (3) bottom sediments; (4) stream animals; (5) animals and plants from tributary swamps, ponds, and lakes. In small brooks certain animals, like trout, depend largely on organisms that fall from the banks; in great rivers food may be nearly lacking in one place and very abundant in another. Forbes (1919) points out that the productivity of a river in fishes is directly related to the degree to which the river overflows its banks, foods thus being made available. Richardson (1921) found that the amount of nitrogen in the bottom mud in the Illinois River was several thousand times that contained in all the bottom-inhabiting animals. Most of the animals that live in streams are poikilothermal, and hence their consumption of food varies considerably with variations in temperature. This and the fact that much of the food in streams comes from outside sources make it difficult to estimate accurately the amount necessary to maintain the animals in different habitats. The writer (1924) has calculated that a freshwater fish consumes about ten times its own bulk of natural foods each year.

Crozier and Harris (1922) studied the animals that lived on a sewage filter and in each cubic centimeter of material found 100,000 protozoans, 3,500 nematodes, 4,000 rotifers, and 150 annelids. Turner (1918) investigated a small, sewage-laden stream and found a "sewage carpet," or "false bottom," of organic material. This was densely populated by protozoans, worms, midge larvae, podurans, etc., and furnished a feeding ground for minnows, turtles, frogs, ducks, and other birds.

Economic Relations of Streams.—The streams in any region are valuable to men as highways, sources of food, and receivers of the wastes from human activities. They are well suited for the latter function because their continual flow and the normal activities of certain of their inhabitants enable them to purify themselves after they have traveled a comparatively short distance. The pouring of wastes into a stream may be a legitimate use or an abuse. If materials are poisonous or in any other way injure the fauna of a stream, they should not be placed in it but disposed of in some other way. Many products now wasted so as to destroy stream animals may be made of commercial value if they are saved (Shelford 1918*b*). Sewage in a river

often increases the number of animals present but does not so affect the plants (Purdy 1923). The warmer branches of the Ohio River that enter from the south have disposed of much more of their organic matter than the colder streams from the north. The "purification" of a river is accomplished through dilution, sedimentation, insolation, oxidation, and the activities of bacteria, plants, and animals. It is usually more rapid in swifter streams. Baker (1920) states that sewage drove snails out of the Genesee River and that when it was reduced the snails returned. Forbes and Richardson (1908) observed that clean-water animals retired downstream when sewage was introduced into the Illinois River; fishes also left the upper part of the river. In an acid stream (pH 5.8–7.2) Jewell (1922) found that clams, certain fishes, and shrimps persisted, but branchiate snails and certain immature insects were absent. Careful surveys and estimates of fishes and fish foods have been made of several rivers in New York (Moore 1927, 1931, 1932).

FORMATION 1. RAPIDLY FLOWING STREAMS

Speed in the movement of streams is, of course, due to differences in level. Mountain brooks "tumble down," and springs "boil up," because water "tends to seek its level," or to move toward a condition of stability. The greater the difference in level between source and resting place, or the steeper the declivity down which water moves, the swifter it goes. Swift-flowing water is usually well aerated; even when containing little plankton it may, by its very speed, bring enough food so that sessile animals may be supplied. As an animal habitat it has the disadvantages that come with the impact of moving water and the objects that it carries along; also those that are due to the great difficulty that attends locomotion or the maintenance of constant spatial relations with the environment.

ASSOCIATION *a*. SPRINGS

Spring Animals and Fascies.—Springs are characterized by constant temperature, which usually shows little variation throughout the year. Those that support an abundant population are usually cold, hot springs usually contain few animals. Over the surface move water striders and whirligig beetles, which feed largely on insects that have fallen on the water from land

habitats (Fasciation 1). There are few swimming animals, except an occasional minnow or stickleback and amphipods (Fasciation 2). Under stones caddis-fly larvae, stone-fly larvae, isopods, flatworms, and snails hide during the day but forage about in the open at night. Depending on the swiftness of the water, the cases of caddis-flies may be fastened firmly to the bottom (Fasciation 3) or freely carried about. In springs themselves there are usually few plants, but cress and other emergent vegetation may grow at the margins. Such plants give shelter to fishes, air-breathing insects and their larvae, crustaceans, frogs, and other animals. In spring pools (Fasciation 5), where water may be rather quiet, considerable vegetation may grow, and types that are usually found in swift-flowing water may be replaced by those that are more characteristic of ponds. Along the margins of springs, in sand or mud, burrowing dragonfly or May-fly nymphs and oligochetes may be found (Fasciation 6).

Animals in Various Types of Springs.—In winter, springs furnish retreats for hibernating animals. Often the space beneath each stone is crowded with frogs which remain sluggish and inactive but do not freeze. Intermittent springs have a scanty animal population consisting largely of ubiquitous amphipods, isopods, snails, and insect larvae. Constantly flowing springs usually have faunas consisting of a few species adapted to the peculiar conditions in each (Huibault 1931). Warm springs usually contain few animals, because gas content is low and dissolved minerals may be present. The rat-tailed maggot and other air-breathing insects are characteristic. Many of the insects in hot springs resemble those that have invaded seas and brackish waters (Brues 1928, 1929, 1932, Hoeppli 1932).

Association *b*. Brooks

Conditions in Brooks.—Brooks are characterized by swiftness, but the current at the bottom and sides is much less than that in the center near the surface. The spaces beneath stones (Fasciation 3) and occasional pools (Fasciation 5) furnish regions of comparative quiet, and some true brook animals require such habitats. Hankinson (1922) states that pools and shore vegetation are essentials in the habitat of the brook trout. A brook usually consists of alternating rapids (Fasciation 3) and pools, and some animals that frequent the one are seldom found in the other.

Beavers build dams across brooks and thus secure ponds which give them a more or less constant water level, space for transportation and storage, and a refuge from enemies. Some brook animals live under or among, not on or above, stones. Usually there is little or no submerged vegetation (Fasciation 4) except occasional patches of Cladophora. As a result of his extensive studies of the biomes in torrential streams in India, Hora (1930)



FIG. 76.—A spider that lurks along the shores of brooks in the mountains of Colombia.

has proposed a different classification from that presented herewith and gives a more important place to attached vegetation.

Limiting Factors in Brooks.—Temperatures in brooks are usually somewhat more variable than those in springs, and some animals are confined to regions near headwaters because it is cooler there. Trout (Creaser 1930, Embody 1922, Powers 1929), planarians (Fulinski 1933, Voute 1929), and insect larvae (Scheffler 1932) are rather definitely segregated into zones by water temperatures below and above 19°C. Brook trout live in

cool waters; rainbow and brown trout persist in brooks that range from 19–24°C.; but no trout live in warmer waters. Of course cool water can carry more dissolved gases than warm, but the distribution of some brook animals, such as blackfly larvae (Wu 1930) and planarians (Voute 1929), appears to be influenced

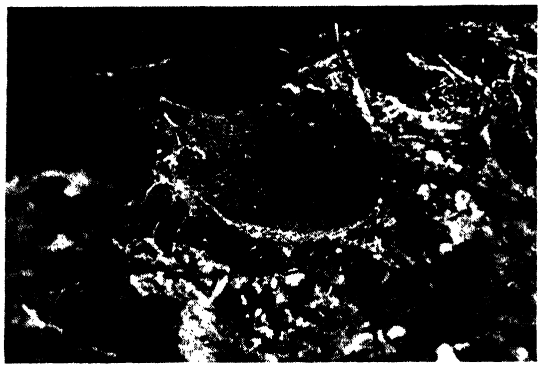


FIG. 77.—Fishing net of a caddis-fly larva, Hydropsyche. (*Photograph by L. D. Wooster.*)

largely by currents and very little by oxygen tension. In mountain streams Powers (1929) found that temperature, pH, and alkali reserve decreased with altitude but that oxygen increased. Brook trout tolerate pH's ranging from 4.1–9.5 and are limited chiefly by temperatures (Creaser 1930); blackfly larvae require swift currents and die when they are absent even when oxygen

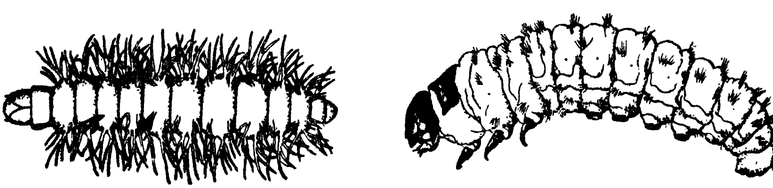


FIG. 78.—Lepidopterous larvae. *Nymphula vittatis* lives in a case in quiet water and bears many gills; *Cataclysta midas* lives in a torrent, builds no case, and has suckers on four of its ventral segments. (*From Tsuda* 1936.)

and ionization conditions are favorable (Wu 1930). Intermittent brooks are unfavorable for snails and other brook animals; but under accumulations of leaves in the dry, stony bed of a woodland brook Needham and Lloyd (1916) found living crane-fly larvae, stone-fly nymphs, amphipods, and earthworms, the last washed into the stream from land. Baker (1919) found snails estivating

in cracks in the bed of an intermittent stream during a drought. The chemical reaction of a brook may be of importance for the animals in it; it has been suggested that trout die after forest fires because the usual slightly acid reaction of the stream has been changed by the wood ashes that wash in from the burned areas.

Characteristic Brook Animals.—The animals that are typical of the rapids in brooks are the nymphs and larvae of caddis-flies, May flies, stone flies, beetles, lepidopters, black flies (Simulidae), and other Diptera; also flatworms, mites, and snails. In pools and under stones and logs lurk fishes (trout, miller's thumb, dace, certain darters, catfishes), hellbenders, amphipods, isopods, crayfishes, crabs, atyids, Sphaeridae. In mountain torrents in Colombia the writer (1915) found no crustacean fauna but only a little catfish and a spider. When the brooks reached the foothills, however, atyids were commonly found in patches of drift; crabs, fishes, and the curious lizards of the genus Basiliscus lurked in the pools; and a dragon-fly nymph burrowed along their shores. In the lowlands, where the streams lost their momentum, shrimps and prawns were common.

Adaptations of Brook Animals.—Brook animals are adapted in various ways to withstand strong currents. Insect larvae may have suckers on their gills, legs, or ventral surfaces so that they can hold on; their legs are often provided with hooks. Black-fly larvae have enormous adhesive organs at the posterior end. The mountain-brook catfishes mentioned in the last paragraph are provided with spines along their ventral surfaces; some brook fishes, like certain gobies in Hawaii, have ventral suckers; the coronchos in Venezuela (Pearse 1920) adhere to the undersides of stones by means of their sucking mouths. Some lepidopterous larvae live under sheets of silk which they spin on rocks. Most of the clinging animals have "streamline" forms and rest with their larger end upstream, but a few are flattened, and one May-fly nymph is described as being shaped somewhat like the blade of a chisel so that the current against its anterior end or legs forces it against the substratum. The animals that move about are strong swimmers (darters, trout, dace) or never release their hold when moving. Black-fly larvae fasten a thread along the bottom and cling to this while they reattach their posterior sucker. A number of animals

seek shelter under objects in the stream and in some cases dig out hollows under the downstream side of stones. The male horned dace constructs a long pile of stones and rests in a depression at the downstream end. Females deposit eggs in the depression; the male covers them with stones and makes a new depression. In this way the eggs are protected from enemies and moving bodies. In the brooks in northern South America there is an insect that deposits patches of eggs on boulders in swift streams, and it is remarkable that these are always on the down-

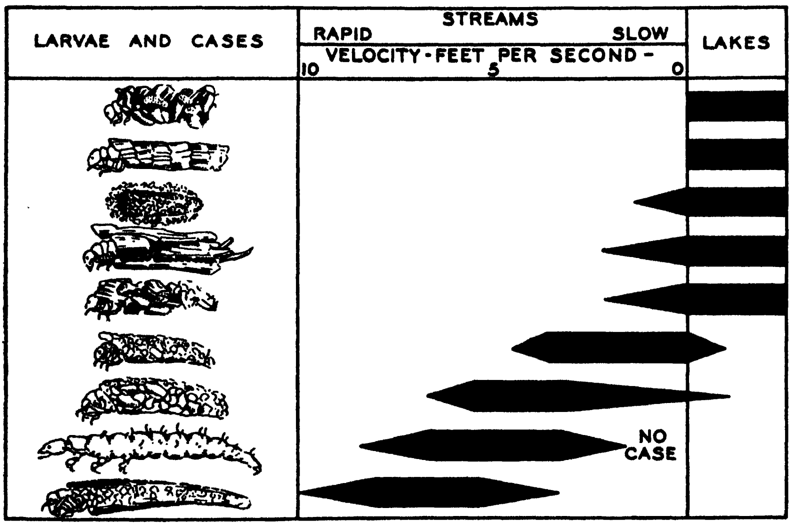


FIG. 79.—A series of caddis-fly larvae from quiet and swift waters. (*Adapted from Dodds & Hisaw* 1925*a*.)

stream side, where they will not be injured by floating objects if there is a flood. Caddis-fly larvae escape from floods, silt, and enemies by living in cases which in swift water are firmly attached. Shelford (1914*a*) studied the behavior of typical animals from rapids and found that there was agreement among them in preference for hard bottom and reactions toward currents, but lack of agreement in behavior toward light. The last was probably correlated with the fact that some of the animals normally live beneath stones, and some in the open. However, toward the two most important factors of brook environment (current and hard bottom) there was general agreement. Many brook animals are nocturnal or crepuscular, hiding during the

day but coming out to forage at twilight. Insects that live in rapids when emerging from the pupal state commonly rise rapidly to the surface and quickly fly away.

Respiratory Adaptations.—Swift currents make good aeration, and brook animals are adapted to water having a high oxygen content. Stone-fly nymphs have very small gills and very little ability to live where oxygen is deficient. Dodds and Hisaw (1924) found that the area of the gills of May-fly nymphs in

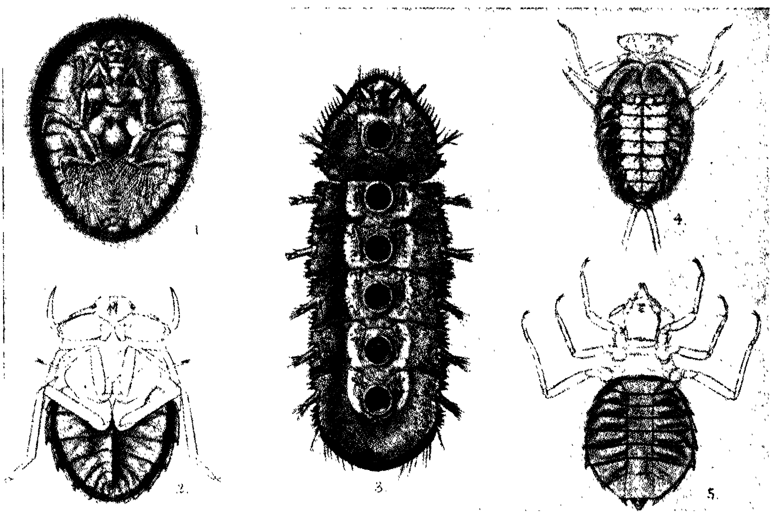


FIG. 80.—Insects, larvae, and nymphs from torrents. 1, beetle larva which uses a marginal fringe of hairs and legs for attachment; 2, bug with spinous pads and median, backwardly directed spines; 3, fly larva with six median suckers, lateral spines, spinous pads, and papillae; 4, May-fly nymph with gill lamellae forming a rim and spinous pads; 5, flat, sprawling dragonfly nymph with six pairs of spinous pads. (*From Hora* 1930.)

mountain brooks varied inversely with the amount of oxygen in the surrounding water but had no very close correlation with the swiftness of currents. Frogs and tadpoles that live in swift streams have reduced lungs and breathe largely through their skins. Some frogs also have papillate dermal gills (Allen 1922). Tadpoles commonly have suckers and roughened clinging surfaces beneath their heads but breathe little or not at all through their mouths (Noble 1929). Several brook fishes use their mouths primarily for clinging and feeding. They cannot let go of the rocks to which they are attached, or they will be

swept away. Such fishes often have separate incurrent and excurrent openings into their branchial cavities (Hora 1932).

Food of Brook Animals.—Many of the inhabitants of rapids catch their food in nets. The quantity of plankton in brook water is usually small, but the swiftness of the current enables plankton feeders to strain much water and continually stirs up sediment that may serve as food. Certain caddis-flies are expert net spinners. Some of these feed on floating algae and animal plankton. They reach out from their cases and scrape off their nets at intervals. Others prey on living food and are ever ready to pounce on anything that may land in their nets. Black-fly and May-fly larvae fish with the nets that are formed by the

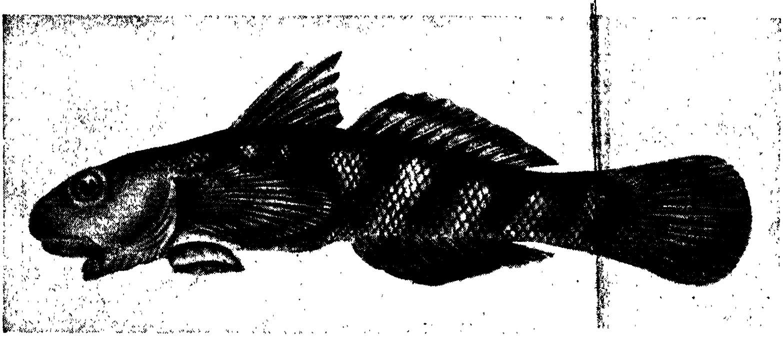


FIG. 81.—A goby, *Riacichthys aspro*, from a torrent. It has papillae about the mouth and a sucker formed from the ventral fins. (*From Hora* 1932.)

bristles on their mouthparts. Atyids' nets are on the claws of their walking legs. Not all dwellers in rapids are net fishers, however. Lepidopterous larvae feed largely on filamentous or encrusting algae; May flies forage for a variety of foods. In crevices and pools predaceous stone-fly nymphs, crayfishes, catfishes, darters, trout, etc., wait for their prey. In Colombia the writer became acquainted with a spider, with an enormous expanse of legs and a ridiculously small body, that rested along the banks of brooks and at intervals ran out over the surface and captured some floating insect (Fasciation 1). In other parts of the earth, water striders and whirligig beetles often rest in eddies along brooks and feed on the insects that continually float down on the surface. Certain fishes that cling to rocks have special papillae and denticulate surfaces for scraping encrusting algae off surfaces and egesting them (Hora 1930, 1932).

Waterfalls.—Waterfalls are extravagantly developed rapids, and there is general similarity between the animals that live in the two habitats. There are some animals, however, that are particularly associated with cataracts. The water ousel builds its mossy nest beneath falls. Leathers (1922) states that he found the larvae of the midges of the family Orphnephilidae only

> . . . on a series of "giant steps" where a small stream spreads out over broad and nearly horizontal stones in its precipitous descent. Here the larvae were found more frequently on the vertical than the horizontal surfaces of the ledges.

Waterfalls are barriers to the migrations of most swimming animals, but some, like the salmon, are able to leap up considerable distances. Eigenmann (1912) describes a fish in Guiana that climbs waterfalls:

> The method of ascent of vertical walls by members of the genus *Rivulus* . . . is of great interest. One of these fishes taken in Shrimp Creek jumped against the vertical face of a huge rock and clung by the adhesion of its tail. *From this point by another flop it made and clung to another point much higher up the face of the rock.*

Abbott (1870) says that lampreys are able to "suck their way up" the vertical facing of dams. A basin at the foot of a cataract is often an excellent fishing ground, because streams serve as highways, and animals journeying upstream tend to collect below the fall. In India, Hora (1931, 1934) has made excellent studies of the animals of waterfalls and their adaptations, especially concerning the little flies of the family Blepharoceridae.

FORMATION 2. SLOWLY FLOWING STREAMS

Creeks and rivers differ from springs and brooks in the rate of flow of their waters. This means a lower gradient in the channel and a correspondingly finer, softer, muddier bottom, because a slow current can move only small particles. Slow current and muddy bottoms permit aquatic vegetation to flourish where the water is not so turbid as to cut off sunlight. Erosion silt in streams cuts off light from deeper parts, decreases absorption of radiant energy, settles over the bottom as a blanket of mud, and retains organic materials that may make conditions of life unfavorable (Ellis 1936).

Association *a*. Creeks

Characteristics of Creeks.—A creek is a small stream that does not flow swiftly and therefore has a muddy bottom. Cowles and Schwitalla (1923) found that the carbon dioxide in a creek varied considerably in different regions and was highest in ponds that occurred in the course of the stream.



Fig. 82.—A creek in British Guiana. (*From Carter* 1934*a*.)

In ponds the pH is modified by the aquatic fauna and flora. . . . When water flows slowly over decaying vegetable matter the pH is lowered. When water flows rapidly over a clean bed, most noticeably at falls and rapids, the pH is raised, probably as a result of aeration. These facts may be readily correlated with the carbon dioxide content of the water. Hence, in this creek, the free carbon dioxide content seemed to be a determining factor in establishing and maintaining pH values. . . . Stagnation of the water and low but uniform pH seem to be two of the factors that determine the distribution of Euglena.

Many creeks are fed from peaty or swampy areas. They therefore often have an acid reaction, and their deeper parts may be deficient in oxygen (Carter 1934, Jewell 1922). At times water is dark in color. This makes it absorb light rapidly, and a

creek therefore usually supports fewer submerged plants than a pond or a lake.

Animals of Creeks.—Certain animals are commonly associated with creeks. Water striders and toad bugs run over the surface;

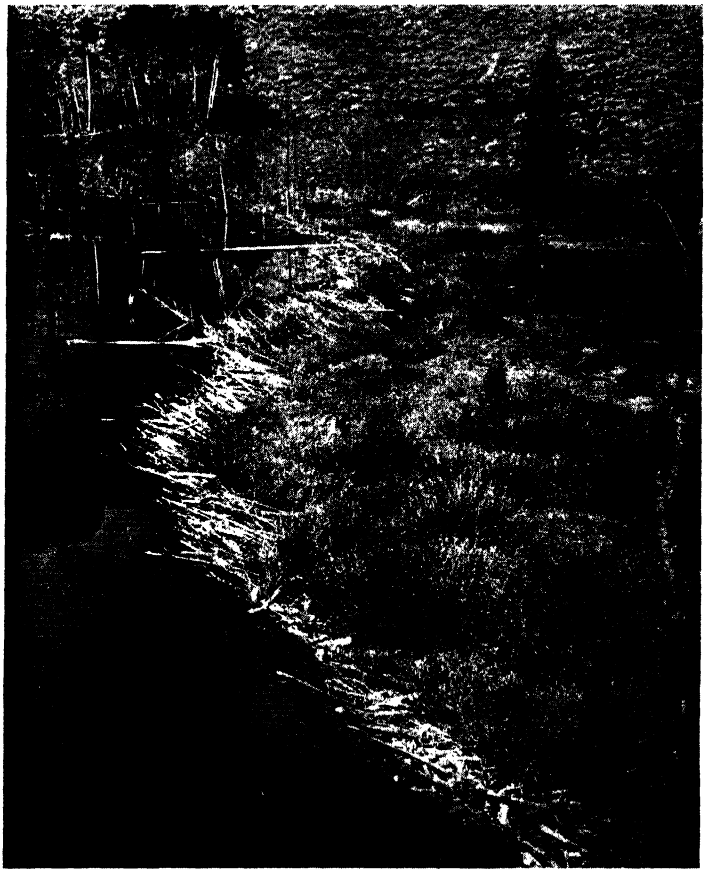


FIG. 83.—A beaver dam across a stream in Yellowstone Park. (*From Warren 1926, courtesy of Roosevelt Wildlife Experiment Station.*)

beavers bring in green branches from the trees near at hand; muskrats and carp grub out roots along the shores; crocodilians, herons, bitterns, ducks, geese, turtles, frogs, eels, dogfishes, bullheads, mudminnows, beetles, odonate nymphs, water bugs, leeches, and hydras hunt for living animals; tadpoles, sunfishes,

suckers, breams crayfishes, amphipods, and snails feed on vegetation and mud or eke out an existence as scavengers; plankton is often present in considerable quantities, and certain species of plankton organisms that do not occur in open water may be abundant. In a creek in southern Illinois (pH 5.8–7.2) Jewell (1922) found numerous shrimps and clams but no branchiate snails or ephemerid nymphs. Creeks in British Guiana (Fig. 82) contained little plankton (Carter 1934). There were few rotifers,

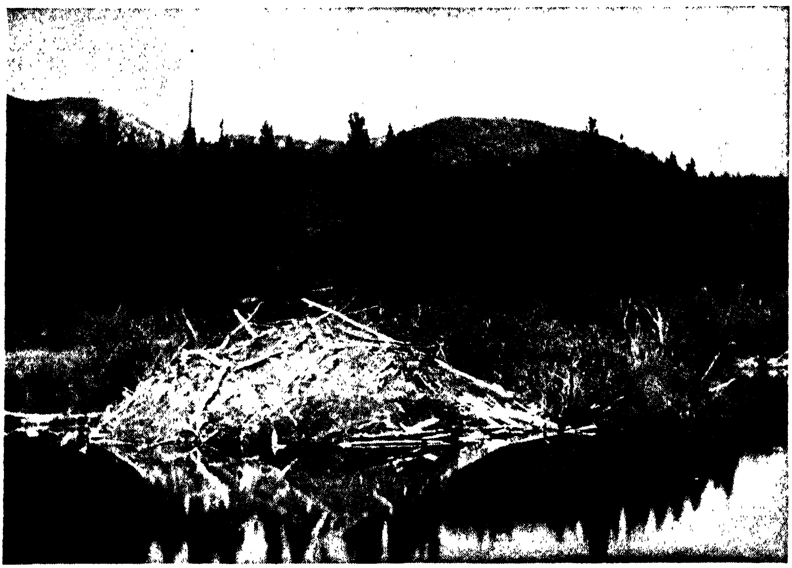


FIG. 84.—A beaver lodge in Estes Park, Colorado. (*From Warren* 1926, *courtesy of Roosevelt Wildlife Experiment Station.*)

but rhizopods were relatively abundant. During the dry season algae increased in numbers. Creeks, like other streams, show variation in the height of water. During floods many animals resort to the submerged plants in the stream or rest in the emergent vegetation along the banks. In winter, turtles, frogs, insects, snails, and leeches hibernate in the mud at the bottom or at the stream margins. Amphipods and some other forms remain active throughout cold seasons. During droughts many creek animals seek pools or remain in the mud under masses of vegetation. Iguanas use creeks as a refuge from danger. When threatened, they dive from the trees where they usually forage,

swim under water to the opposite bank, sneak out into the underbrush, and are seen no more. Beavers build dams (Fig. 83) across creeks and thus create ponds (Warren 1926). These serve as refuges and highways for the transportation of food, which is stored in the bottoms of their ponds. Beavers live in lodges (Fig. 84). Like most animals that occupy permanent homes they are infested with external parasites and have a specially modified louse claw for combing their fur.

Association *b*. Rivers

Characteristics of Rivers.—A river, on account of its large volume, the fluctuation in the amount of water passing over its stream bed, and rate of flow, varies considerably in its area. Its connection with tributary swamps, lakes, sloughs, and smaller streams gives it important functions as a highway to feeding and breeding grounds and as a refuge during periods of cold or drought. Its turbidity prevents light from penetrating very far, and there are many more animals near the surface than at greater depths. Muttkowski (1918) found a scanty population in the turbid main channel of a river studied by him but an abundance of animals in the clearer water near the banks. Lakes in the courses of rivers serve as settling basins for suspended materials and serve to equalize the flow of water, and rivers with large lakes in their courses are therefore not changed to such an extent by floods as those without. The temperatures of rivers may vary more than those of smaller streams on account of seasonal changes, variation in the amount of water received from tributaries, height of water, amount of insolation, etc. Kofoid (1908) found that, when the temperature of the Illinois River fell in winter to 7°C., the plankton decreased 90 per cent from its summer maximum. A flood may reduce the oxygen content of a stream as much as 50 per cent, probably largely because silt and organic materials are brought in from bottom lands; and fishes may then die in great numbers (Forbes 1911). Rivers that drain lakes usually contain less carbon dioxide than mountain streams or lowland rivers (Powers & Hickman 1928). The Nile River is an example of a great stream that receives varying amounts of water from its tributaries at different seasons (Fig. 85), and conditions in it vary accordingly.

Animals of Rivers.—Though river faunas are largely derived from tributary habitats, and though many of the animals that live in rivers are also found in other habitats or live in rivers only part of the time, there are many true river animals that are seldom or never found elsewhere. For example, in the Mississippi drain-

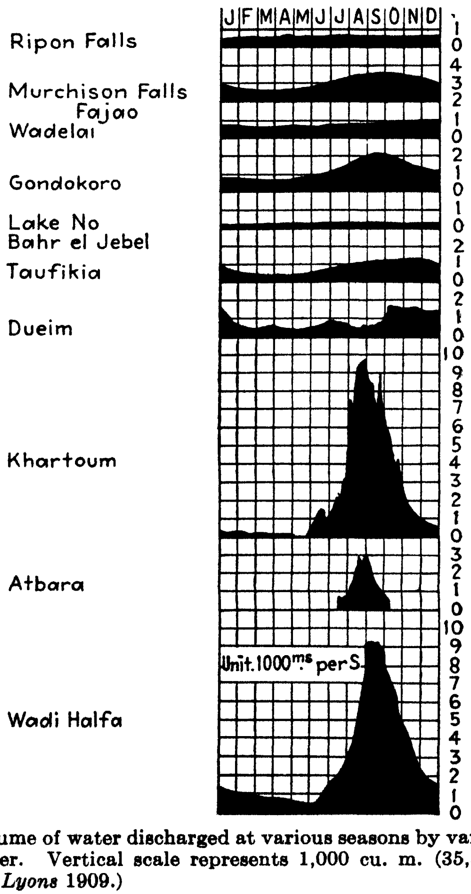


FIG. 85.—Volume of water discharged at various seasons by various tributaries of the Nile River. Vertical scale represents 1,000 cu. m. (35,300 cu. ft.) per second. (*From Lyons* 1909.)

age there are four gigantic fishes (mud cat, rock sturgeon, alligator gar, spoonbill), quillbacks, mooneyes, several minnows, gizzard shads, mussels, softshell turtles, and other animals that do not invade small streams. For the most part the typical river animals are (1) fishes and turtles that are strong swimmers, (2) heavy-bodied mussels and burrowers that can withstand the

strong currents, shifting bottoms, and accumulating drift. In the Ganges River is a dolphin that never enters the ocean. Some tropical river systems have indigenous crocodiles and caimans. There are some insect larvae that are quite characteristic of rivers (Roach 1933). River communities are not so inconstant and variable as many ecologists have believed. Though they show variations with seasonal progressions and with differences in height of water, they maintain some stability (Shelford & Eady 1929).

Fasciation 1. River Bottoms.—River bottoms above the usual stream channel are inundated only at time of high water but are tributary to the river itself. Forbes (1919) has called attention to the importance of the backwaters of rivers as places for the digestion and assimilation of foods and has expressed his opinion that the production of food fishes in a river is more or less directly related to the area that may be overflowed. Garman (1888) made a careful study of the animals in the Mississippi River bottoms. He found raccoons present at all times, ascending into the trees at times of high water. There were comparatively few birds, snakes, or amphibians, and no tadpoles; but in the ponds and sloughs there were many turtles; insect larvae and nymphs (midge, caddis-fly, dobson, stone fly, May fly, damsel- and dragonfly); bugs; fishes from sloughs, creeks, and rivers; bryozoans; hydras; protozoans; and a few snails. In the vegetation were spiders (Tetragnatha), mites, grasshoppers, and crickets. In the tropics foxes, lizards, and crabs often hunt over river bottoms. In all climates grazing animals also commonly invade the bottoms to feed. Floods enable fishes (Fasciation 5) and other aquatic animals to forage in habitats that are usually not available to them. The writer once caught a bullhead that had eaten a nestling of a bird and on another occasion examined a carp that had gorged itself with grass.

Fasciation 2. Shore Animals.—Shore animals are abundant, both in and out of the water. Some land animals come to the shore only to drink and are awaited by predaceous crocodiles and piranhas which seek to devour them. There is a drift line which, though not so clearly defined as along lakes, is sought by various scavenger insects, birds, and other animals. The writer has shown (1921) that at one point on the Mississippi in summer there are more fishes, both in variety and numbers, in shallow

water than in any stratum at greater depths. This is probably due to the turbidity and currents, which prevent the growth of plants except in very shallow water, and thus fishes that are associated with vegetation are often caught while taking the shortest route from one feeding ground to another. Young fishes commonly seek the shallows alongshore to escape from their enemies.

Fasciation 3. Surface Animals.—The animals that rest on the surface are well represented in rivers by loons, ducks, grebes, gulls, and other water birds, but there are comparatively few insects. Though whirligig beetles are perhaps more abundant along rivers than elsewhere, there is, in general, a scarcity of water striders and other insects that are so characteristic of ponds, swamps, and small streams. These surface predators tend to collect at the mouths of tributaries, where currents are not too swift and where food continually floats down from other habitats which have more direct connections with productive areas.

Fasciation 4. Potamoplankton.—The plankton of rivers has already been discussed (p. 310) to some extent. A considerable portion of it is derived from backwaters and tributaries. The continual movement and turbidity kill many plankton organisms, which settle down after dying and enrich the bottom. Kofoid (1908) characterizes river plankton as (1) polymixic, (2) fluctuating in quantity and constitution, (3) lacking characterization by any particular species but with a large proportion of littoral species. "Channel plankton of the Illinois River, therefore, has its source in a large degree in impounded backwaters, and is maintained to a considerable extent by their run off." Steuer (1910) describes bacteria, diatoms, protococci, desmids, and rotifers as typical of river plankton. He divides different types into (1) eupotamotic, consisting largely of rotifers; (2) tychopotamotic, derived from quiet water and containing many crustaceans; (3) benthopotamotic, bottom organisms (Oscillatoria, diatoms, Arcella, etc.) swept away by currents; (4) pseudopotamotic, textile and muscle fibers, and detritus; (5) autopotamotic, organisms that normally live in flowing water (Micrococcus, Sarcina, Bacillus, etc.). He also states that plankton is influenced by the source, swiftness, length, tributaries, backwaters, turbidity, and contamination of a river and by seasonal changes. Kofoid (1903)

found that the plankton of the Illinois River reached its maximum quantity in April, May, and June and its minimum in January and February. Allen (1920) observed an autumnal maximum in the San Joaquin River. Two hundred thousand tons (wet weight) of plankton pass Havana in the Illinois River each year. This amount is 60–150 times that of the average weight of bottom animals. The nitrogen in the water is 92–232 times that contained in its net plankton (Richardson 1921). Typical lake plankton after it enters rivers rapidly disappears, especially where there are areas of aquatic vegetation (Chandler 1937). As streams grow larger and more species of plankters are present, more of them occur at all seasons (Eddy 1934).

Fasciation 5. Swimmers.—The swimmers in rivers are mostly fishes and, particularly in the tropics, large shrimps and prawns. Crocodilians, hippopotami, in some places sharks and dolphins, are also represented. In going from headwaters to the mouth of a river the number of species of fishes increases (Shurrager 1932). Some tropical river fishes are able to live for considerable periods in mud when left stranded by falling waters (Hora 1933). Other fishes that live on muddy bottoms carry their eggs in their mouths (Smith 1931).

Fasciation 6. Bottom Animals.—On shifting bottoms there are usually no plants in the river bed. However, Richardson (1921) in his careful survey of the Illinois River found that bottom animals were most abundant on mud near aquatic vegetation. Howard (1919) surveyed the entire bottom on a 3-mile section of the Mississippi and reported that, in general, animals were restricted to a 200-ft. zone along each shore and to a narrower strip around islands. This distribution had no apparent relation to depth, for the middle of the river was not deeper than the zones nearer shore. The most productive areas in this case, in which the survey was primarily directed toward mussels, were strips near shore that were swept by strong currents. Mussels, according to Allen (1921), feed almost continuously, and largely on nannoplankton, so they would derive very apparent benefit from currents. Over a stretch of 59 miles of river, Richardson (1921) found that bottom animals were most abundant on muddy bottoms where there was least current. Molluscs made up 31–99 per cent of the bottom animals, which (without considering calcareous shells) weighed 10.4–5,196 lb. per acre. Richardson

observed, however, that the fauna of aquatic plants of swampy margins and of lakes connected with the river greatly exceeded that on the bottom of the river itself. The weight of the flesh of the animals associated with vegetation averaged 2,118 lb. per acre; that of those on the bottom, 255 lb. Settled plankton furnished the chief food for snails, caddis-fly larvae, Sphaeridae, and other bottom animals. Lakes connected with the river were frequently favorite feeding grounds for fishes, and the amount

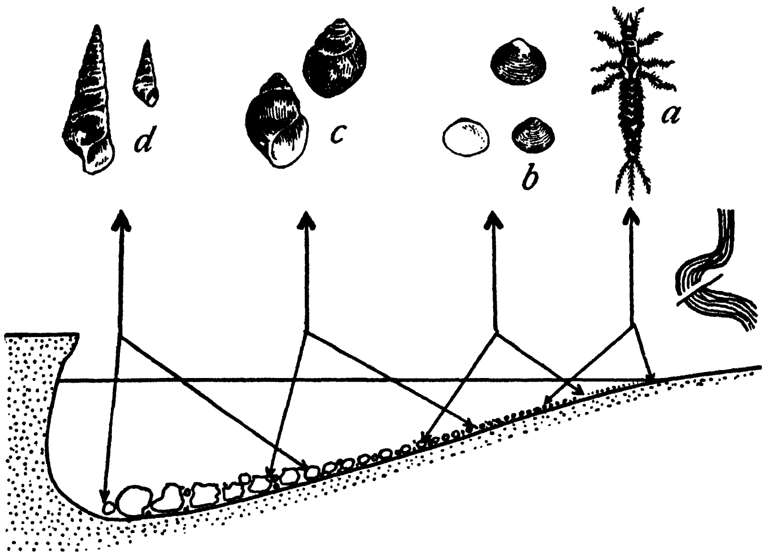


FIG. 86.—Assortment of animals at the bend of a stream. At the left a bank is being eroded by swift currents; at the right mud is being deposited. *a*, burrowing May-fly nymphs, Hexagenia; *b*, small clam, Sphaerium; *c*, viviparous snail, Campeloma; *d*, river snail, Pleurocera. (*From Shelford* 1913.)

of food available on the bottoms of such lakes was approximately five times as great as that on the bottoms of comparable glacial lakes in Illinois. Some animals that are associated with the bottoms of large rivers are also present on the bottoms of certain lakes: sturgeon; mussels; operculate snails; large, burrowing May-fly nymphs. On the bottom of a canal Baker (1918) collected 116 mussels in an area measuring 10 by 15 ft. Floods destroy bottom animals in rivers, but areas where animals survive are rather quickly repopulated, types with shortest life histories coming in first (Moffett 1936) and according to the usual laws of succession (Gersbacher 1937). Pollution may also destroy cer-

tain types but may increase others by furnishing food (Ludwig 1932).

River Bends.—At river bends bottom animals are usually assorted according to the swiftness of the current. On the outside of the bend are snails and other animals that frequent harder bottoms. In midstream live such animals as burrowing nymphs and clams, which can flourish on shifting bottoms but require currents for the bringing of their food. On the inside of the bend, where the bottom may be muddy and even support aquatic plants, conditions approach those in swamps, and such animals as pond snails, Sphaeridae, and frogs may be present. In deep holes in rivers, particularly if there is little current, conditions may approach those in lakes, but many of the characteristic animals of the depths of lakes are not present because rivers seldom show a great degree of thermal stratification, and deep water is not much cooler than that at the surface.

PROVINCE B. STANDING WATERS, LENTIC HABITATS

Quiet vs. Flowing Waters.—Of course, there is no such thing in the world as absolutely quiet water, but lakes, ponds, pools, and swamps differ from streams in that their waters flow little or not at all. The standing waters of the earth are again readily separable on the basis of their size and depth, lakes and ponds with their greater volumes and exposed areas being more subject to the action of waves and currents, whereas pools and swamps are generally stagnant. There are many aquatic animals that cannot exist in environments where there is wave motion. A mosquito larva, for example, must live in stagnant water because surface disturbances prevent the protrusion of its breathing siphon, and suffocation results. Other animals are limited in their distribution to habitats where there is continual wave motion or to bodies of water where wave motion is possible. Water pennies live under the pebbles and boulders on wave-beaten shores. Ciscoes flourish in lakes that have sufficient size and depth to furnish cool, deep, oxygenated water at all seasons.

Subprovince B(a). Lacustrine Habitats

Among freshwater habitats lakes have been most studied by biologists.

Characteristics of Lakes.—Lakes resemble oceans in their general features but, of course, differ from them in their small size, the presence of definite boundaries on all sides, and their very low salinity. As a habitat for animals they are not so unvarying as the ocean but are the most stable of freshwater habitats. Forbes (1887) fancifully but properly described a lake as an "island" containing older life in the midst of newer land life. Compared with the land, a lake in many respects does support a more primitive fauna. Its animals are also isolated and closely related and, on the whole, present little variety. Muttkowski (1918) has set forth the conditions and characteristics of lake life as follows: (1) depth and area enough for wave action; (2) lack of emergent and floating vegetation (on account of wave action); (3) absence of plants, except Cladophora, along the shore line and the presence of peculiar, flattened, clinging, and burrowing animals; (4) a dearth of animals that breathe air at the surface; (5) a plant zone (which varies with the transparency of the water and with seasonal changes) along the shore and a group of animals that varies in numbers with the plants; and (6) striking thermal stratification and a corresponding distribution of organisms. All lakes are subject to periodic oscillations in level or seiches. These are initiated, maintained, and modified by sun, moon, atmospheric pressure, and winds. Though they never attain the proportions of marine tidal movements, they do induce shore currents and cause changes of a few inches in levels. In Lake Erie, Krecker (1931) found seiches with periods of a few minutes to several hours. These produced currents in littoral habitats and thus influenced the temperature, reaction, transparency, and other conditions in littoral habitats. Lakes also differ markedly in temperature on account of depth, contour, shape of basin, shores, solutes in water, color, and other features.

Types of Lakes.—Birge (1907) in his classic paper on the "respiration of an inland lake" points out that lakes, like organisms, have periods of birth, youth, maturity, old age, and death. Besides such a physiographic cycle, lakes also have individuality —each taking its character from its drainage basin, climate, shape, area, depth, gradient of its slopes, solutes in its water, vegetation, animals, etc. From a biological point of view depth is perhaps more important than contour or shape of basin. In general, the shallower a lake the more productive of life it is.

Depth also functions in another way by allowing thermal stratification in the water and, where it is sufficient to cut off the lower water from contact with the atmosphere during all or part of the year, may lead to regularly recurring periods of stagnation in deep water. Various classifications have been proposed for distinguishing different types of lakes, but perhaps the most comprehensive and successful were those of Forel (1892–1904) and Whipple (1898), who distinguished polar, temperate, and tropical lakes and subdivided each class according to periods of vertical circulation or "overturn" and the relation between bottom and surface temperatures. Birge and Juday (1911) and Thienemann (1922) have made some modifications of Whipple's original scheme. At present lakes may be divided into the following groups:

I. Polar—temperatures never above 4°C.:
- Type 1. Bottom remains at 4°C. throughout the year; one circulation period possible in summer, but usually none.
- Type 2. Bottom temperatures fluctuate but remain near 4°C.; one circulation period in summer.
- Type 3. Bottom temperatures close to surface temperatures; water circulates more or less continuously except when frozen.

II. Temperate—temperatures vary above and below 4°C.:
- Type 1. Bottom temperature remains at 4°C. throughout the year; two circulation periods possible in spring and autumn, but often none.
- Type 2. Bottom temperature fluctuates but remains near 4°C.; two circulation periods in spring and autumn.
- Type 3. Bottom temperatures close to surface temperatures; water circulates throughout the year when the surface is not frozen.

III. Tropical—temperatures always above 4°C.:
- Type 1. Bottom remains near 4°C. throughout the year; may be one circulation period in winter.
- Type 2. Bottom temperature fluctuates but remains near 4°C.; a circulation period in winter.
- Type 3. Bottom temperature close to surface temperatures; water circulates more or less continuously.

Most lakes of type 1 are over 200 ft. deep; those of type 2 are usually more than 25 ft. deep; and those of type 3 are usually less than 25 ft. deep. There are many variations in types of lakes. In Japan, for example, there are organogene and mineralogene acidotrophic types (Yoshimura 1933), depending on

whether organic or inorganic acids are significant. Yoshimura has proposed a classification of lakes based primarily on oxygen content.

Lake Temperatures.—Probably temperature is the chief factor in determining the "climate" of lakes, as it is of land habitats. It also sets a general limit for the rate of metabolism and thus may limit the total amount of life that may develop in a particular lake. Wesenberg-Lund (1905), Shantz (1907), Coker (1911), Dodds (1917), and Haempel (1918) all agree that there is less plankton in alpine lakes than in those of the lowlands. Dodds (1917) classifies lakes in Colorado as alpine, montane, and plains, largely on the basis of temperature differences. Haempel (1918) states that most plankton species in alpine lakes are probably perennial. Altitudinal lines between lakes are not

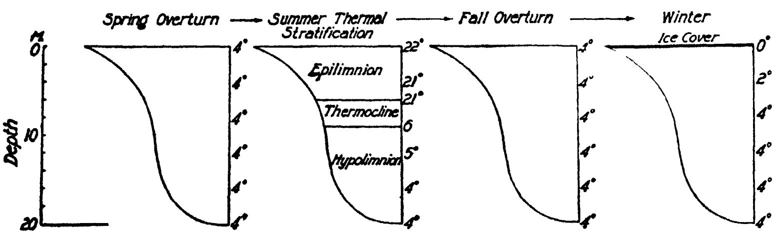


FIG. 87.—Showing temperatures, degrees centigrade, in a deep lake in temperate regions at the four principal seasons. (*From Welch* 1935.)

always sharply drawn on account of size differences. A large lake warms and cools more slowly than a small one and may support a greater variety of life because it is capable of furnishing a wider range of temperatures. In most lakes plants and animals are on the ascendant in spring and summer when available light and heat are increasing. In autumn there is usually a diminution; storms destroy and wash much of the attached vegetation away. In winter many animals are in a state of torpor and of repressed activity. Some insects become active before the ice leaves a lake in the spring (Muttkowski 1918). As in other formations, the inhabitants of lakes are adjusted to normal climatic seasonal rhythms in each latitude. Deep lakes that are protected from winds have lower temperatures in deep parts than those which are more subject to such circulating influences. In temperate regions the temperatures of very deep lakes remain slightly below 4.0°C. at all seasons. In winter shallow lakes may

become much colder than deep lakes because they are overturned to a greater extent (Yoshimura 1936). Limnologists have lately come to consider "heat budgets," or the amount of heat required to raise a body of water from winter to summer temperature, as a significant factor in determining the character and productivity of lakes (Welch 1935).

Deep and Shallow Lakes.—The depth of a lake determines its character to a considerable degree. A shallow lake warms and

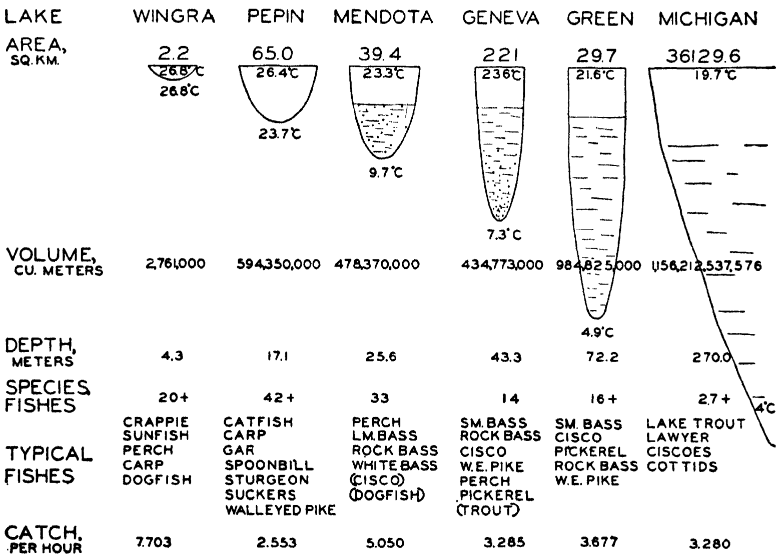


FIG. 88.—Conditions and dominant fishes in six Wisconsin lakes in summer. Lake Wingra is really a pond. The small circles in the hypolimnions of Lakes Mendota and Geneva indicate that oxygen is wholly or partly absent. (*From Pearse* 1934*a*.)

cools quickly, may support standing vegetation in all its parts, is easily made to circulate from top to bottom by winds, and hence rarely shows thermal stratification. A deep lake usually has a high degree of stratification with warm water above and cold below. In summer, deep lakes are usually divided into three rather clearly defined strata: (1) an upper *epilimnion*, which is warm and circulates when moved by winds; (2) an intermediate *mesolimnion*, or thermocline, which is often only a meter or two in thickness and in which there is a rapid change in temperature; and (3) a deep, cool *hypolimnion*, in which there is a very gradual decrease in temperature toward the bottom. A shallow plant-

choked lake usually supports more fishes and other aquatic animals per unit of area than a deep one, but the latter usually has a greater variety of species. There is apparently some factor that limits the levels at which animals live. For example, in Wisconsin, lakes up to about 100 ft. in depth have the bottom dominated by yellow perch; but in lakes that are deeper, ciscoes are usually dominant. In Lake Michigan both perch and ciscoes are abundant, but the former are never taken in deep water. Lake Pepin, which is an expansion of the Mississippi River, and Lake Michigan are both rich grounds for commercial fishermen,

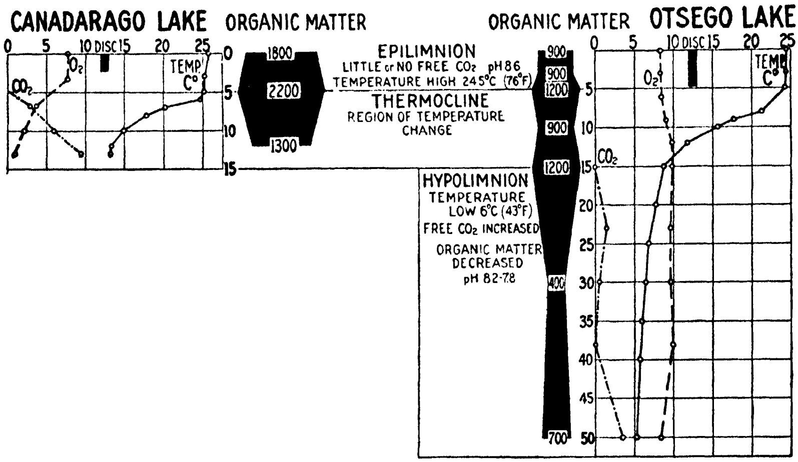


FIG. 89.—Contrast between a shallow and a deep lake in New York, July 1935. Organic matter is shown in milligrams per cubic meter; chemical data, in parts per million; depths, in meters; and temperatures, in degrees centigrade. (*From Tressler & Bere* 1936.)

but the former yields mostly carp, red horses, buffalo, and quillbacks, whereas the latter supplies trout, ciscoes, and whitefishes (Pearse 1921, 1934*a*).

Transparency of Lakes.—Transparency of the water in various lakes varies greatly. The zone of photosynthesis may thus be limited to a couple of meters near the surface or extend down through 10 m. or more. A stratum of optically pure water 1 m. thick absorbs 60 per cent of the sun's energy. Observations on 470 lakes in Wisconsin showed transparencies, as judged by the disappearance of a white disk when lowered, from 0.3–13.6 m. Transparency was correlated with transmission of solar energy and varied with color of water and the presence of particles in

suspension (Birge 1913, Juday & Birge 1933). Less than 20 per cent of the sun's energy penetrates to a depth of a meter; in turbid lakes the amount may be as low as 2.5 per cent. The zone between 1 and 2 m. usually absorbs 40 to 50 per cent of what passes through the upper stratum. The amount of solar energy below 6 m. is usually "too small to be measured," and 1 per cent of the sun's energy rarely reaches 5 m. In Green Lake, however, which is one of the clearest in Wisconsin, 1 per cent is present at 7 m. There is always correlation between transparency and permeability. The depth to which light

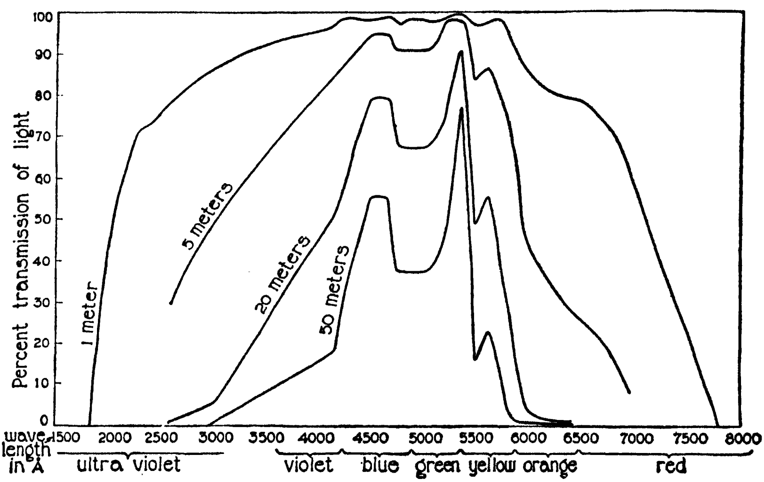


FIG. 90.—Graphs showing the percentage of transmission of light of various wave lengths at various depths in pure water. (*From Welch* 1935.)

penetrates, of course, controls the quantity of plant life that can develop in a lake. By suspending bottles containing water and algae the optima for photosynthetic activity at various depths in Wisconsin lakes has been determined (Juday & Schomer 1935, Schomer & Juday 1935). Maximum activity varied between depths of 4.0 and 10.0 m. The percentage of utilization of solar radiation by algae increased with increasing depth and reached a maximum where total radiation varied from 1.2 to 8 cal. per centimeter in a 3-hour period. "In Crystal and Trout Lakes, maxima were found where 57 per cent of the solar energy fell in green and yellow spectral bands, but 78 per cent of that at 1 m. in Helmet Lake was in the red band." The vision of fishes is efficient at very low intensities (Clarke 1936),

and hence fishes may see well at considerable depths. The writer (1921) has shown that in turbid lakes there is a greater variety and quantity of fish life in the first 5 m. below the surface, but in clear lakes there may be more species and greater numbers of fishes between depths of 5–10 m. than in the surface stratum.

Gases in Lakes.—Depth and transparency modify other aspects of lake ecology besides photosynthesis and thermal stratification. The dissolved gases are profoundly influenced. Birge (1907) points out that a lake carries on respiratory processes

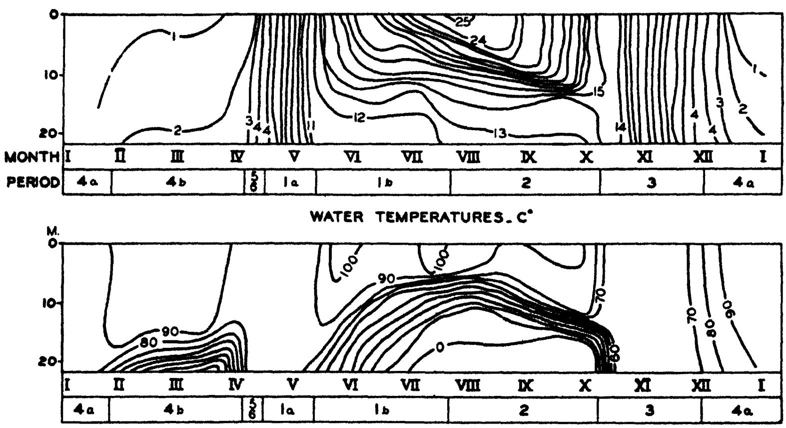


FIG. 91.—Depth and seasonal distribution of temperatures and percentages of dissolved oxygen in Lake Mendota, plotted according to Yoshimura (1935):

1*a*, half summer stagnation period } Summer stagnation period
1*b*, summer complete stagnation period }
2, summer partial circulation period
3, autumnal whole circulation period
4*a*, winter half stagnation period } Winter stagnation period
4*b*, winter complete stagnation period }
5, winter partial circulation period
6, vernal whole circulation period

during which gases (chiefly oxygen, carbon dioxide, and nitrogen) are exchanged with the atmosphere. In winter the oxygen usually decreases in lakes of temperate or cold climates, and carbon dioxide increases because such respiration cannot take place on account of ice. In a deep lake the going out of the ice in spring is followed by the vernal overturn; all the water is thoroughly mixed and aerated at all depths. After a few warm, quiet days the upper portion of the lake becomes warmer than that below, and an epilimnion is thus established. As the summer progresses, the hypolimnion, being cut off from contact with the atmosphere, loses oxygen and acquires carbon dioxide

through the respiration of animals and the decay of organic materials. Finally, there may be no oxygen left, and many animals die or migrate into the epilimnion where oxygen is present. In many lakes water becomes supersaturated with oxygen in the region of the mesolimnion (Juday & Birge 1932). In autumn the epilimnion gradually cools, and when it reaches the temperature close to that of the hypolimnion the autumnal overturn takes place, and the water throughout the lake is again aerated from top to bottom. If a coating of ice cuts off contact with winds, the lake becomes stratified again in winter, and its deep water may again lose its oxygen. When the deep waters of a lake become stagnant, the animals living in them must be able to endure considerable periods without oxygen or migrate. Perch move to high levels but swim down into the stagnant zone at times to feed. They can live for as much as 2 hours in water without oxygen and draw to some extent on oxygen stored in their swim bladders (Pearse 1920*a*). Corethra larvae migrate up into the epilimnion at night and return to the hypolimnion during the day (Juday 1921). Sphaeridae that live through periods of stagnation apparently do so by remaining wholly inactive, but chironomids, oligochetes, and protozoans are able to remain active for as much as 3 months in water without oxygen. Plankton distribution is not closely correlated with the quantities of gases present. Plankton animals do not at once leave regions where oxygen is decreasing, but where oxygen is less than 0.1–0.2 cubic centimeter per liter there is usually no living zooplankton. This usually means that in lakes that stagnate there are few or no zooplankters below the mesolimnion; but sometimes in a clear lake after a period without wind, oxygen may extend below that stratum or in a turbid lake not extend down to it. Corethra larvae and some apparently anaerobic protozoans are able to swim about in stagnant water without injury. Noland (1925) says:

> A group of species, *Colpidium colpoda, Glaucoma pyriformis, Glaucoma scintillans,* and *Paramecium caudatum,* were observed to occur most abundantly in infusions of high bacterial content where oxygen was almost or entirely absent.

In surface samples from 510 lakes in Wisconsin oxygen varied from 3.4–12.4 mg. per liter of water, or 34–129 per cent of satura-

tion. The smallest amounts were found in bog lakes (Birge & Juday 1932).

Animals in Lakes.—A characteristic group of animals inhabits lakes. Some of these animals are also found in other habitats, but some are found nowhere else. Ciscoes, lake trout, lawyers, and whitefish are familiar examples of the latter group. Necturus has well-developed external gills and breathes from water, whereas its relative Cryptobranchus, which lives in streams, comes to the surface for air continually when kept in quiet water (Willey 1920). This characteristic lake amphibian is ecologically "more a fish than a salamander" (Pearse 1921*b*). The peculiar crustaceans Pontoporeia and Mysis are not found in freshwater habitats, except in the depths of lakes. Johansen (1922) in his discussion of arctic habitats says:

> Perhaps the best criterion for what may be considered a lake and what a pond in this vicinity, there being all grades between them, is the presence of the typical and common freshwater amphipod (*Gammarus limnaeus*) which is not found in ponds, but only in lakes and their tributaries. . . . Their occurrence is thus an interesting contrast to the other large freshwater crustaceans (Euphyllopoda), which principally occur in ponds, lagoons, or smaller lakes along the Arctic coast.

Each lake and even each stratum has characteristic species and races of animals (Eddy 1934). In artificial lakes in Italy cladocerans usually attain final dominance but are sometimes wholly absent. Their development is dependent on algae and not correlated with that of copepods (Brunelli 1930). Races of Daphnia segregate at different levels; "some associations belong to the epilimnion, others to the thermocline, and still others to the hypolimnion" (Woltereck 1932). Fishes (Fig. 88) vary in size, coloration, and other qualities in different lakes (Pearse & Achtenberg 1920, Pearse 1921).

Quantity of Life in Lakes.—Alm (1922) has classified lakes according to their dominant species and the food resources present. His work will be discussed later in connection with bottom animals (p. 361). In most lakes the maximum quantities of plant and animal life come in the summer. Rickett (1922, 1924) and Juday (1924) have made a careful survey of the shore plants and plankton in two Wisconsin lakes, Green and Mendota. In Green Lake, which is clear and deep (70 m.), the shore plants

extended to a depth of 8–10 m. and averaged 15,180 kg. (1,780 dry) per hectare; in Mendota, which is rather turbid and of moderate depth (27 m.), the average yield was larger, 17,778 kg. per hectare. In Green Lake 9 per cent of the plants grew between 0 and 1 m.; 42 per cent, between 1 and 3 m.; and 49 per cent, between 3 and 8 m. Chara constituted 49 per cent of the dry weight of the plants; in Mendota, Vallisneria produced about one-third of the total weight. The total plankton in Green Lake

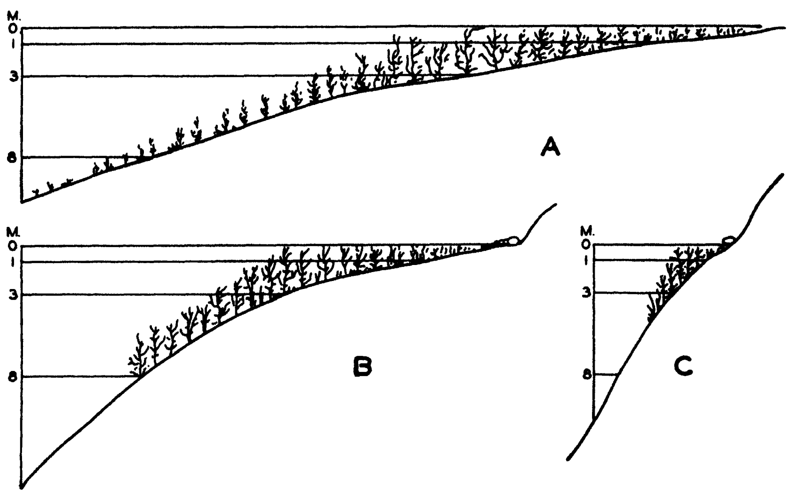


Fig. 92.—Distribution of plants on gentle (*A*), medium (*B*), and steep (*C*) slopes on lake shores. (*After Rickett* 1924.)

weighed (dry) about 818 mg. per cubic meter of water, or about 27 g. per square meter of surface.

Results obtained in Lake Mendota indicate that about one-third of the organic matter of the net plankton is derived from rotifers and the crustacea, the two forms which are most concerned in the consumption of other organisms. . . . The organic matter in the total plankton which might serve as food for the rotifers and crustacea would weigh about fifty times as much as that found in these two forms of plankton organisms.

In Green Lake the total weight of the bottom fauna was about one-tenth that of the total plankton. These figures give some idea of the food resources in a rather rich lake (Mendota) and a deep, cold, and rather barren lake. Bacteria in Lake Mendota fluctuate at different seasons and with changes in environment

(Fred, Wilson & Davenport 1924). In shallow lakes, which are really ponds, plants and animals may occur in enormous quantities. Algae and other plants may cover the bottom and provide food for many invertebrates (*e.g.*, Baker 1918, 1924).

Productivity of Lakes.—The ability of a lake to produce organic food, of course, depends on a variety of factors. A lake with much shallow water above the mesolimnion, thus furnishing good opportunity for decomposition in warm water, will produce more plankton than a deep lake with a bottom that descends rapidly from the shore line (Birge & Juday 1911). The capacity of a lake for food production depends on both materials and proper conditions. The temperature, turbidity, amount of available carbon dioxide, or other substances may limit the rate at which photosynthesis may take place. Some deep lakes apparently do not have enough carbon dioxide in summer to produce much plankton, even though many types of algae are able to convert bicarbonates into carbonates in order to obtain it. The factors that contribute to the productivity of a lake are so complex that it is, of course, not possible to say that carbon dioxide is the sole limiting factor in such cases. Atkins (1923*a*) has shown that phosphates in ponds decrease greatly in April, until they are practically absent; and (1923*b*) that silica decreases greatly as it is used up by diatoms. In most lakes the greatest amount of plankton is in surface strata. In his study of shore animals in Lake Mendota, Muttkowski (1918) found that insects constituted 60 per cent of the macrofauna. Land insects that fall into lakes also may make material contribution to food resources. The important foods may vary in different types of lakes, and the total amount of food may limit the number of animals that can live. The writer (1921*a*) has compared Lake Mendota, which is rich in fish foods, with Green Lake, which is rather poor, and has shown that the former supports twice as many fishes per unit of area as the latter. In Lake Mendota (1920*a*) the yellow perch eat about equal quantities of insects and entomostracans, but in Lake Wingra, which is shallow and contains much vegetation, few entomostracans are eaten. In Lake Pepin, which is an expansion of the Mississippi River, the chief fish foods are plankton, mud, and crayfishes; in the inland lakes of Wisconsin, fishes feed mostly on plankton, fishes, insects, and molluscs; in the depths of Lake Michigan, the fishes depend largely on other fishes and crusta-

ceans that swim near the bottom (1921). More species of lake fishes feed alongshore than elsewhere; more feed on bottom organisms than on those of the open water. Considering all types of lakes, the important *fish foods* are plants, small fishes, insects, entomostracans, and bottom sediments (1918).

Fred, Wilson, and Davenport (1924) have studied the seasonal variations of bacteria at various depths in Lake Mendota. Numbers ranged between hundreds and thousands per cubic centimeter on account of fluctuations in rainfall, wind, temperature, the physical and chemical condition of the water, and other factors. High numbers were found to be due not only to the multiplication of lake bacteria but also to the presence of bacteria that had been washed in from soil and other sources. Variations in temperature had little effect on the multiplication of lake bacteria, and sunlight appeared to inhibit their growth very little. As a rule, there were fewer bacteria in the lake than could have existed on the available food. Domogolla, Juday, Peterson, and Fred (1925) have shown that the waters of Lake Mendota contain:

> . . . more than nine times as much soluble nitrogen as total plankton nitrogen. . . . There is seasonal variation in the different forms of nitrogen found in Lake Mendota. . . . Ammonia, nitrites, nitrates, amino-acids, and proteins reach a maximum in winter and fall to a minimum during the summer. A sudden and marked increase in ammonia and nitrates occurs in February. The bottom water always contains more of the different forms of soluble nitrogen than the surface water. . . . The seasonal variation in the different forms of soluble nitrogen indicates that these compounds form part of the nutrients of both plant and animal life of these waters.

The quantities of different protein compounds were also determined. In Lake Mendota and other lakes in Wisconsin "the average dissolved protein is from three to six times as great as that of the plankton; the dissolved nonnitrogenous material is about 10 times as great" (Birge & Juday 1926). In Norway, Strom (1933) studied a lake which consisted of two parts. Rotiferans and cladocerans were equally abundant in both parts, but copepods were three times as abundant in one part which was twice as productive as the other. Productiveness appeared to be related to greater depth and nitrate content.

Classification of Lakes on Basis of Productivity.—Limnologists commonly classify lakes in three groups, largely with reference to productivity, depth, and oxygen content (Welch 1935, pp. 312–313). They may be briefly characterized as follows:

Oligotrophic—deep; little shallow water; transparent; small amounts of nitrogen and phosphorus; little of suspended or organic materials; oxygen at all depths; few shore plants; little plankton; often rich bottom fauna, with marine relicts and peculiar deepwater fishes.

Eutrophic—shallow; with shoals; transparency low; rich in nitrogen, phosphorus, and calcium; rich in suspended and organic

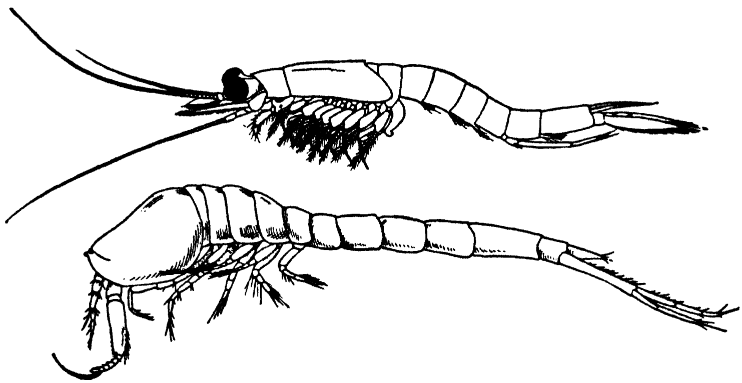


FIG. 93.—Two marine relict crustaceans, *Neomysis intermedia* (Czerniavsky) and *Lamprops korroensis* Dershavin, from the depths of Japanese lakes on the Kurile Islands. (*From Miyadi* 1937.)

materials; oxygen often absent in deep water in summer (and winter); many littoral plants; rich plankton; bottom animals few in species but often numerous; no peculiar deepwater fishes.

Distrophic—deep or shallow, in bog surroundings or in old mountains; yellow to brown in color, not transparent; little phosphorus, nitrogen or calcium; much humic material; often lack of oxygen, especially in deep water; usually little plankton; few deepwater animals, mostly insect larvae.

Zonation of Lakes.—The zonal arrangement, so characteristic of the animals that live in lakes, is due primarily to three factors: wave motion, the depth to which light penetrates, and temperature. Wave motion disturbs the water to varying depths (1–5 m. or more), which are generally correlated with the area of the lake, and sweeps the shore clean. "Where the interaction

of waves and returning undertow is greatest" is the breaker line, or rachion (Muttkowski 1918). Above this the beach on wave-beaten shores is devoid of plants, and below it the vegetation extends in a zone of varying width, which depends on the slope of the bottom and the turbidity of the water. The maximum depth to which vegetation extends in the clearest lakes is about 25 m. Thermal stratification may separate a deep lake into epilimnion, mesolimnion, and hypolimnion; once such separation is brought about, oxygen may become deficient in deeper strata and thus prevent certain animals from living there. Stratification and zonation in the distribution of animals in lakes are usually striking phenomena. In Green Lake, Juday (1924) found the greatest variety and smallest number of bottom animals between depths of 0 and 10 m.; the maximum number, 20–40 m.; and the smallest variety, 40–67 m. In the same lake the writer (1921*a*), fishing with gill nets in summer, found all species of fishes in the lake, except the cisco, between 0 and 10 m.; from 10 to 20 m., only pickerel, suckers, and largemouthed black bass were caught; between 20 and 40 m., only ciscoes. In Lake George, Needham (1922) found the maximum number of insect larvae at 36 m., and of oligochetes at 50 m. The zoning and stratifying factors usually divide lakes into: (1) a littoral region which extends down to a depth of about 10 m.; (2) a deepwater bottom region below 10 m.; and (3) an open-water region in the middle of the lake. The littoral is divided into zones: the beach above water, submerged beach, breaker line, plant zone (which may be subdivided into several strata). It ends where light and wave motion cease to be potent. In the deep, bottom region live animals that are adapted to ooze and often also to stagnation. The open water in lakes of sufficient depth is separated into two distinct regions by the mesolimnion.

FORMATION 1. LITTORAL REGION

The littoral region of lakes, like that in the ocean, varies greatly according to exposure to wave action, light, character of bottom, extent of shallow water, solutes and suspended matter in water, temperature, vegetation, and other factors. Its depth also varies in different lakes. In Lake Geneva, Switzerland (Forel 1892), it may reach down in certain situations to more than 25 m.; in Lake Mendota (Muttkowski 1918) it extends to about

7 or 8 m.; and in very turbid lakes it is even thinner. Muttkowski's classification of bottom zones in Lake Mendota is as follows:

Littoral (phytal):
  Eulittoral (euphytal):
    1. Shore line: 0 to 1 meters; rocky, stony, or sandy, barren. Shoals: 0.5 to 1 meter.
    2. Surf line (rachion): 1 meter; stony, barren.
    3. Vegetation zone: 1.5 to 6 meters.
       Upright vegetation: 1.5 to 5 meters; Potamogeton, Najas, Vallisneria.
       Recumbent vegetation: 4 to 6 meters; Chara, Myriophyllum, Ceratophyllum, Potamogeton.
       Barrens.
       Rock reefs: 3 to 8 meters; plant marl, stones, rocks with encrustations.
  Sublittoral (dysphytal):
    4. Shell zone: 6 to 8 meters; shell, sand, barren, mud and decaying organic matter.
  Aphytal:
    5. Aphytal zone: 7 to 25 meters; mud, etc.

Muttkowski uses "littoral" as synonomous with "phytal," which is very proper in a lake like Mendota, where the depths of the zone of photosynthesis, the region of wave activity, and the epilimnion are practically the same; but in very turbid lakes the phytal zone may be thinner than that of wave action, and in clear, small lakes it may be thicker. At the head of a bay there may be no shore-line zone, and the vegetation zone may come to the edge of the water, the conditions becoming like those of swamps. Along Isle Royal, Gleason (1909) observed that snails were confined to bays on account of wave action. In Lake Oneida, Baker (1918) found the greatest development of plants above the 6-ft. contour line, and 88 per cent of the molluscs present were also above it. In Winona Lake, Headlee (1906) described the range of the mussels as extending from the shore to the beginning of soft mud. Allen (1922) states that mussels are restricted to the epilimnion chiefly by currents, temperature, dissolved gases, and especially the character of the bottom. In general, Muttkowski's scheme fits lake shores very well. He does not consider the land immediately above the water line, however, which, as it is kept bare by storms and the pushing up

of ice, is included by many writers among lake habitats as a littoral zone or zones. Muttkowski has been a purist in his classification, excluding muddy shore lines because he interprets them as swamps and omitting what physiographers call the upper and middle beaches because they are not submerged. The "upper beach" is beyond the limit of the action of waves and ice and forms a transitional area to the land habitats above; the "middle beach" may be invaded by ice in winter and waves during summer storms, but is above the surface of the lake when the water is quiet; the "lower beach" is covered by water and is subject to strong wave action. Demel (1923) from studies in Lake Wigry proposes to divide littoral regions into three zones: (1) wave action, (2) submerged vegetation, and (3) sublittoral.

Littoral Animals.—A characteristic but varied group of animals lives in littoral habitats. Depending on the character of the bottom, vegetation, waves, and other factors, there are swimmers, burrowers, clingers, climbers among plants, etc. Many caddisfly larvae have flattened cases and thus are not readily rolled over by waves; waterpennies escape the impact of moving water by their flatness and the extreme thinness of their edges. Chironomids are able to live in sandy beaches by spinning threads to fasten the shifting grains together and quickly build new shelters when rendered homeless by storms. The food relations of littoral animals are diverse. There are scavengers, predators, phytophages, etc. The phytophagous species are, of course, largely associated with the shore vegetation. In the zone below the vegetation the majority of the animals are detritus feeders. The physiological adjustments of animals to shore waters are as varied as the habitats. Some animals live in soft mud where there is little oxygen, and others spend their lives on wave-swept rocks. There are also many special adaptations for reproduction. Altogether the shore animals constitute a group of great variety, with specializations for various modes of life but often showing considerable unity in special habitats. On the shores of Lake Erie, Krecker (1933) carefully surveyed the distribution of animals down to a depth of 6 ft. Chironomid larvae were more abundant than other types. The greatest numbers occurred at a depth of about 18 in., where there were 4,000 animals per square yard. Between 1 and 6 in. there were 2,500; between 36 and 72 in., 500 per square yard.

Association *a*. Hard Beaches

Firm bottoms are developed where strong currents or waves continually sweep the shore and prevent the deposition of fine sediment. In such situations a number of animals live, and many are adapted in various ways to withstand or take advantage of the conditions associated with moving water, but there is little in freshwater habitats that is comparable to the barnacles, mussels, and other animals that live along the shores of the ocean on the exposed surfaces of rocks where they are subjected to the full force of waves. All the hard-bottom animals along lake shores live in crevices or beneath stones, where they are more or less continually in turbulent water but are not struck directly by waves or by the objects moved by them. Clay beaches are either rather barren where wave swept or, where they are in quiet water, are soon invaded by aquatic vegetation and converted into muddy-bottom habitats. Rocky shores and the wooden structures made by man are the typical hard-bottom habitats in freshwater. The only plant that is abundant and characteristic is the branching, filamentous alga, Cladophora, which is well suited to live in moving water and often shelters many small animals. Other algae (Rivularia, diatoms, etc.) occur and often help in forming calcareous encrustations over the surfaces of rocks.

Fasciation 1. Beaches above Water.—The upper and middle beaches are rather barren regions on rocky shores, particularly if the rock face is vertical or overhangs the water. Cliffs, however, are favorite resorts for certain birds, such as kingfishers and swallows, which seek their food in or above the water. A few transient spiders, ants, beetles, and land snails may hunt over the rock surfaces or hide in sheltered crannies. If the beach slopes up from the lake, it may have a scattered covering of lichens and in the upper part support a considerable variety of flowering plants. Here logs and other drift lodge and furnish shelter for insects (grasshoppers, ants, flies), land isopods and snails, frogs, toads, lizards, spiders, chipmunks, and mice. Some of these animals commonly hunt along the shore line for insects and other stranded organic materials left by the waves. Gulls, crows, and blackbirds also frequently forage in such places. Butterflies and dragonflies fly over open beaches. Pools above the reach of waves on rock beaches usually vary considerably in temperature.

often being warmer than the lake during the day and cooler during the night. Most of the animals in such pools can migrate if conditions become too unfavorable or are easily transported by birds or other wandering animals. The flora usually consists of algae and is scanty. Such animals as hydras, amphipods, entomostracans, immature and adult insects (water boatmen, water striders, caddis-flies, dragon- and damsel flies, dytiscid and hydrophilid beetles), snails (Physa, Limnaea, Planorbis), and shore birds may be present.

Fasciation 2. Shore Line.—Just below the surface of the water there is the most violent wave motion to be found anywhere on lake shores. On smooth rock surfaces there are no animals that live continuously along the shore line, but during quiet weather animals from the vegetation zone below commonly migrate up into this stratum, particularly at night.

Fasciation 3. Rachion.—Where there are stones that are large enough to remain unmoved during storms, the shore line has a flourishing population beneath the stones and among Cladophora growths. Burrowing insects, larvae, oligochetes, leeches, and fishes like the miller's thumb and fan-tailed darter are also more common where the beach consists of separate stones. The fauna on these shores is characteristic and often strikingly adapted to the conditions; leeches and May-fly nymphs are flattened and cling tightly; the cases of caddis-flies are rhomboidal or flattened and may even have lateral flanges to prevent rolling (Molanna); the beetle larvae (Psephenus) are extremely flat; the snails and leeches have large adhering surfaces; the miller's thumb and fan-tailed darter are fishes with big heads and large mouths which lurk in crevices and are able to dart out to capture food. At the breaker line there is little or no accumulation of shells and other heavier materials as on sandy shores, and few animals are present unless there is shelter beneath rocks. If an appropriate substratum is present, hydras flourish best in the upper meter of water in Michigan and Minnesota lakes in summer. They may grow well down to 12 m. in autumn but never migrate into very deep water (Miller 1936). The form of the shells of certain snails varies with the degree of movement of the water on the shores where they live (Geyer 1931).

Fasciation 4. Shore Vegetation.—The animals of the vegetation zone are not very different from those above where there

are broken rocks on a beach, but on smooth rock surfaces there are often heavier growths of algae below the breaker line; and among these, amphipods, snails, and insect larvae find shelter and food.

Fasciation 5. Sublittoral Zone.—The sublittoral zone usually occurs at greater depths on rocky shores than elsewhere because, being exposed on outstanding points of land, the beaches are subject to more violent wave action. Here the tube-dwelling chironomids and oligochetes, burrowing larvae and worms, and snails feed on the accumulated organic materials from zones above.

Association *b*. Sandy Beaches, Psammolittoral Region

On superficial examination sandy beaches may appear to be rather barren, but many such situations teem with life. Usually there are not many species represented, but those present may be numerous and are usually well adapted to the peculiar conditions under which they live (Stangenberg 1934, Wiszniewski 1934).

Fasciation 1. Drift Line.—Sand is a shifting substratum, in water or on land. Along sandy lake shores there are often moving dunes and smaller sand waves which are frequently shifted by winds. On the upper beach, grasses continually overgrow moving sand waves and, when they stop them, are succeeded in the Northern Hemisphere by poplars, willows, and oaks. On the middle beach there is usually an abundance of drift, and this, by furnishing food and shelter, makes conditions favorable for land animals. Spiders, ants, tiger beetles, toads, skunks, and other predators come here to feed. There are also many scavengers that depend on the drift line for food. On the shore of Lake Michigan, Needham (Folsom 1923) counted 4,000 insects in 1 l. of drift. On the same lake, Snow (1902) identified 114 species of insects in drift during a month and a half in spring. She found that the greatest numbers were washed up when an offshore was followed by an onshore wind. Wheeler (1887) pointed out that the insects washed up along the drift line were largely flyers and often nocturnal. Herms (1907) made a careful study of the constituent animals of drift along Lake Erie. After a storm there were 538 fishes per mile. Herms gives a list of scav-

enger insects, among which flies and beetles are important. Along the shores of Saginaw Bay, Lake Huron, Ruthven (1911) found few animals, apparently because logs and other drift were soon covered over by sand. Many burrowing insects live just above the water line on sandy beaches and depend largely on stranded plankton for food (Silvey 1936). The statoblasts of bryozoans commonly sink to the deeper parts of lakes in winter, but a few survive exposure along drift lines or even passage through the enterons of animals (Brown 1933).

Fasciation 2. Animals of Shore Line.—Barren, sandy shoals along the shore line are favorite resorts for young fishes of various species. There are also some dragonfly nymphs that burrow along the edge of the water, and podurans live in or on the sand.

Fasciation 3. Rachion.—The rachion is usually marked by pebbles and shells and is frequented by such fishes as the Johnny darter, which feeds on burrowing chironomid larvae and oligochetes. If there is a considerable extent of shallow water, a bar is usually built at some distance from the shore line. This protects the water on its exposed side from the action of waves, and the number of animals is usually greater on account of its presence. Along the outer margins of such bars, fishes (Johnny darter, minnows, bass) often clear off spaces for nests. Microscopic psammons are arranged in definite zones at various depths in the rachion. Most of these along Wisconsin lakes are rotifers, but harpacticid copepods and tardigrades are also common (Pennak 1937).

Fasciation 4. Submerged Beach below Rachion.—Below the breaker line the miller's thumb may lurk among gravel, and in the sand are oligochetes and chironomids. Caddis-fly larvae which build cases of sand grains and creep about over the bottom are often common; dragonfly nymphs and crayfishes also lie half buried in the sand or forage over the bottom. If plants get a foothold in this stratum, they may gradually dominate it, and mud accumulates among them. Very often a sandy shore line and rachion are succeeded in deeper water by a vegetation zone which has the characteristics of the next association to be described. Mussels flourish on sandy shores but do not live among dense growths of vegetation. On the other hand, snails are rather rare on clean sand but increase in numbers when vegetation is present. Animals (hydra, etc.) and plants may be

attached to the shells of molluscs or to other solid objects that exist on sandy shores, and animals (Hyalella, damsel-fly nymphs, etc.) may live among the plants that grow on such objects. In Lake Oneida, which is shallow, Baker (1918) found that animals were twice as numerous on sandy bottoms as on rocks, but Muttkowski (1918) and Gleason (1909) in large, deep lakes found more animals on rocks than on sand.

Fasciation 5. Sublittoral Zone.—The sublittoral zone on sandy beaches is often made up largely of the shells of molluscs. It is populated by many of the burrowers that live in the zone above. Chironomid larvae and oligochetes form the greater part of the population, but such animals as snails, leeches, amphipods, and caddis-fly and May-fly larvae may be present.

Fasciation 6. Shore Water.—The shore water on sandy beaches is continually contributing plankton to shore habitats; much of this when dead settles into the sublittoral region and serves as food for the animals there.

Association *c*. Muddy Beaches

Muddy beaches occur only where there is little wave movement. They are usually overgrown with vegetation and thickly populated with animal life. The bottom sediments, the large and small plants and animals that grow on them, and the shore water all furnish food resources that are rich in organic compounds. Aeration is not always good, however, especially where there is much decaying material on the bottom or where photosynthesis is cut off below the surface by coatings of floating plants. Animals on mud beaches have abundant food and are in little danger of injury by waves but may easily suffocate if they are not especially equipped for respiration in poorly aerated water. In the accumulations of organic bottom materials there may be oscillatorias, beggiatoas, and fungi.

Number of Animals on Muddy Bottoms.—In Lake Oneida, Baker (1918) estimated the number of animals over muddy bottoms, giving his figures as the average number on 16 sq. in. Between 1 and 6 ft. there were 36.66; 6–12 ft., 2.30; 14–18 ft., 1.52. In Lake Winnebago (Wisconsin), which is 45 km. (28 miles) long and has a maximum depth of 6.38 m. (20.75 ft.), Baker (1924) found animals on the bottom in the following numbers per square meter: boulders 331; gravel 1,578; sand 1,325; mud

1,449; vegetation 4,400; average 1,626. Muttkowski (1918) does not include muddy bottoms in his excellent discussion of the littoral region of Lake Mendota, apparently because he feels that muddy shores are to be looked upon as tributaries but not parts of the lake proper.

Fascies on Muddy Beaches.—The shores above the water (Fasciation 1) are frequented by foraging birds, rodents, insects, and spiders and are favorite resorts for basking turtles. The quietness of the water along muddy shores permits the existence of an abundance of surface animals (Fasciation 2), such as toad bugs, water striders, and gyrinid beetles. Ducks, grebes, and other birds also resort to them to feed. The shore line and rachion (Fasciations 3 and 4) are often poorly developed or absent. The vegetation zone (Fasciation 5) may extend up to the edge of the water and in many cases grades into emergent vegetation, which is characteristic of swamps and may shelter such animals as red-winged blackbirds, swamp sparrows, and rails. The amphibious snails wander in and out of the water; among the plants live snails, insects (bugs, beetles, odonate nymphs, etc.), sunfishes, breams, bullheads, mud minnows, frogs, and turtles. Many of the animals are facultative or obligate air breathers and come to the surface at intervals for respiration. Certain animals (oligochetes, chironomid larvae, nematodes, bryozoans), however, live attached to or resting upon submerged plants. The sublittoral zone (Fasciation 6) on a muddy shore supports the usual group of detritus feeders (snails, sphaeridae, chironomids, etc). In the shore water (Fasciation 7) over muddy bottoms there is usually quite a distinctive group of organisms, many of which are not found in other parts of lakes. There are plankton animals that seldom occur in open waters and species, such as certain rotifers, copepods, and ostracods, which usually creep about on plants. There may be leeches and insect larvae which are usually attached or buried in the bottom. On the whole, the shore plankton animals are less transparent than those of open water.

ASSOCIATION *d*. LAGOONS

Lagoons are cut off from the molar activity of the open lake by bars which support emergent vegetation. They are often more like swamps than muddy shores. The lack of wave motion

is associated with an abundance of surface animals (Fasciation 2). Hall (1924) has described a lagoon where floating plants covered the water so completely that they prevented photosynthesis below the surface; putrefaction and other activities used up practically all the oxygen. Doubtless, similar conditions obtain in many lagoons. There is usually an abundance of plant and animal food, but the water is often poorly aerated.

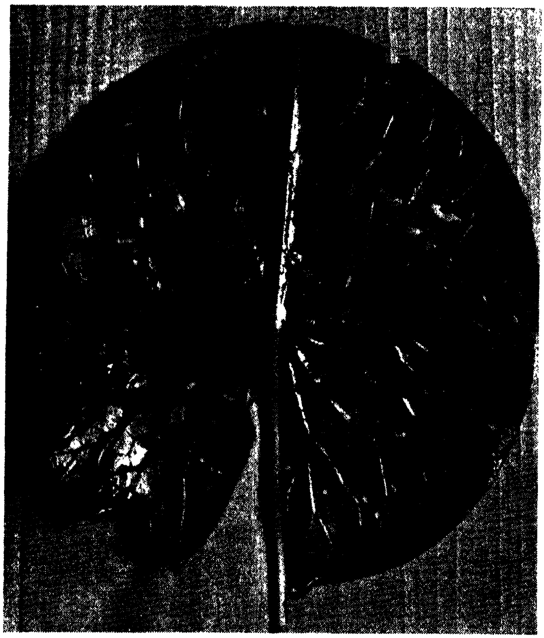


FIG. 94.—Leaf of a water lily showing crescentic groups of eggs and perforations produced by a beetle (Donacia), which sticks its ovipositor through the leaf from above.

Animals in Lagoons.—The animals in lagoons are largely associated with the aquatic vegetation, using it for food or shelter. Turtles and frogs may remain submerged for considerable periods, but the vegetation is thick enough so that it gives them support when they wish to rest at the surface. Jacanas, rails, and other birds commonly run over the floating plants. Insects and snails crawl on the surface or lurk among the plants. Certain plants, like the water lily and cattail, support interesting and characteristic societies. The plankton, as on muddy beaches, differs

from that in open water in the species present and in the greater degree of pigmentation.

Association *e*. Estuaries

Estuaries usually resemble lagoons in having a soft bottom composed of sediment that contains much organic material, but they differ in containing flowing water. The latter peculiarity has marked effect on the animal life. Gyrinid beetles and water striders are usually abundant about eddies where jetsam gathers. The water, on account of its movement, is rather well aerated and contains many plankton organisms that have come from stream habitats. The bottom is often thickly carpeted with mussels. River snails and burrowing oligochetes, chironomid larvae, and May-fly nymphs may be abundant. The vegetation often teems with sponges, hydras, planarians, bryozoans, and insects that depend more or less on flowing water for food and that are not common in lagoons. Certain fishes (breams, tadpole cats, etc.) have favorite resorts at the mouths of streams. Estuaries with sandy bottoms and few or no aquatic plants may be barren.

FORMATION 2. LIMNETIC REGIONS

Limnetic Animals.—The animals that live in the open water of lakes are largely minute mites, crustaceans, rotifers, and protozoans, which, with countless floating plants, constitute the plankton. There are also some nekton animals, such as trout and herring gulls, that frequent open waters. In general, there are few limnetic species in a lake, but there are often enormous numbers of individuals. There seems to be general agreement that there is, as a rule, more plankton per unit of area in freshwater than in the ocean (Johnstone 1908, Lohmann 1911). Probably this is due largely to the lesser extent of bodies of freshwater. In shallow lakes there are undoubtedly more plankton animals per unit of volume than in those of greater depth. Warming (1909) states that the plants of the limnoplankton constitute one of the most cosmopolitan of formations. In deep lakes there are relatively more plankton animals and fewer plants. Steuer (1910) points out that in the lakes of temperate regions diatoms are usually the dominant plants from December to July and that schizophytes lead from August to November. Rotifers reach their

maximum number in summer; crustaceans often have maxima in spring and autumn. The maximum for all plankton plants and animals together usually comes in May in the Northern Hemisphere. In a lake, seasonal conditions in a particular year may make a certain species dominant, but in another year another species may lead. In alpine lakes crustacea often constitute the major portion of the plankton (Juday 1907). Steuer (1910) classifies limnetic plankton as (1) true limnetic; (2) passive limnetic (Heliozoa, etc.); (3) tycholimnetic (brought into open water by winds and currents); (4) merolimnetic (*e.g.*, Chaoborus larvae, which spend much time in bottom mud); and (5) pseudolimnetic (detritus, bodies of insects, etc.).

Adaptations of Plankton Animals.—The limnetic plankton animals are generally transparent, and when pigment is present it occurs as small specks. They often have thin shells and means for flotation (oil, surface film attachments) or for impeding sinking (helmets, crests, spines, etc.). Many of them swim well and without much effort but progress slowly and cannot make headway against strong currents. They are generally adapted to be near but not actually at the surface. Wilson (1917), however, describes larval parasitic copepods which

> . . . have the ability possessed by many of the free swimmers, of holding themselves suspended from the surface film of the water by means of their antennae, their bodies hanging in a vertical position, and they often come to rest in this manner and remain for some minutes.

Wesenberg-Lund (1908) has pointed out that flotation devices wax and wane as the viscosity of the water changes with the seasons. In winter they are least apparent and begin to increase as the water warms and becomes less viscous in the spring. Wesenberg-Lund believes that plankton organisms each year recapitulate their history since glacial times as they change from winter to summer forms (Fig. 13). A review of the taxonomy, ecology, and seasonal variations of European plankters has been published by Rylov (1935).

Limnetic Zones.—The limnetic region of a lake that has a depth of more than about 8 m. shows a rather definite stratification. The thickness of the epilimnion varies with the progress of the seasonal cycle and according to the shape, direction, and area of the surface and the consequent effects of winds. The

effects of waves seldom are felt below a depth of about 2 m., the extent of their influence varying with their height, which, in turn, depends on the size of a lake and the force of the wind that causes them. The zone of photosynthesis varies with the turbidity of the water and the roughness of its surface. The mesolimnion varies in depth and thickness. When a lake is more than 40 m. deep the hypolimnion, even when plenty of oxygen is present, has an upper zone in which there is little life because there is a lack of food. If the deeper water of a

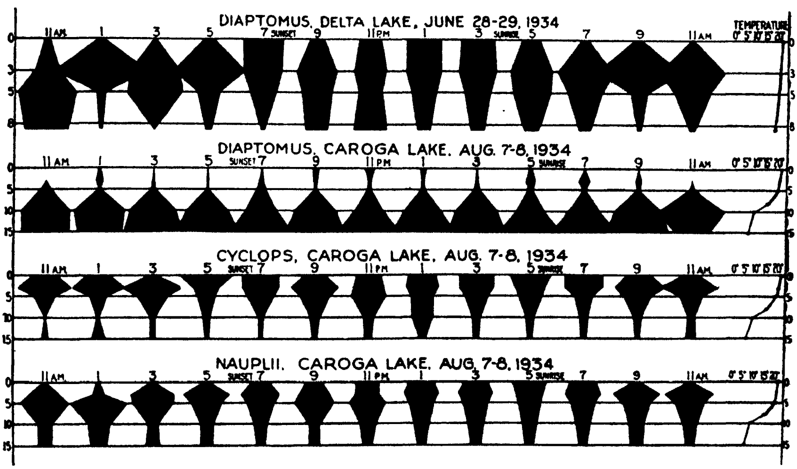


FIG. 95.—Vertical distribution of certain macroplankton crustaceans at 2-hour intervals during day and night in two lakes in New York. Crustaceans are shown as the percentage of total number at each depth; depths, in meters; temperatures, in degrees centigrade. (*From Tressler & Bere* 1935.)

lake stagnates and loses its oxygen, many animals migrate into the epilimnion. When the depth is over 70 m., the whole lake usually is poor in plankton. Many instances of stratification of limnetic organisms have been recorded. Whipple (1896) described the distribution of diatoms. Needham and Lloyd (1916, p. 308) give excellent diagrams that show the distribution of various algae and protozoans. Juday (1912) refers to an interesting observation by Parker in Lake Cocituate: Synura was not found above depths of 4.5 or below 12 m. The limiting factor in this case was believed to be temperature, the range for the organism being 6.4–19.2°C.; and the optimum, 9.2–10.4°C. In an alpine lake, Haempel (1918) found three strata: (1) 0–3 m., dominated by mastigophorans; (2) 3–

10 m., populated largely by cladocerans; (3) 10–40 m., mostly copepods. In Lake Mendota, Birge (1897) found that plankton was rather uniformly distributed in winter, though one species of Daphnia and young Cyclops were more abundant in upper strata. In summer, 44–45 per cent of the crustaceans were in the upper 3 m. The young of nearly all species of crustaceans lived at higher levels than adults. There were most crustaceans of all ages at a depth of about half a meter. Food, temperature, and gases all exerted important influences in distribution; light, wind, and gravity were apparently less potent. Stagnation below the thermocline drove out most of the limnetic animals. Light was important only in the upper meter or two. During the day young crustaceans remained near the surface, thus avoiding competition with older individuals. It was noticed that the latter swam upward with greater difficulty. The young of Cyclops were most abundant near the thermocline. In Green Lake, Marsh (1901) observed that Limnocalanus was characteristic of an intermediate region but occurred above and below in smaller numbers. The depth of the maximum amount of plankton varies widely in different types of lakes, and there is usually little below depths of 35–85 m. (Steuer 1910). Steuer states that stratification usually depends primarily on temperature. In the Bodensee in summer he found Diaptomus and Cylops at all depths; rotifers, Daphnia, and Bosmina were confined to the warm upper stratum (0–15 m.); Leptodora was distributed largely between 7 and 18 m.; in the deep, cold water (15–28 m.) were Heterocope and *Cyclops strenuus.*

Food in Limnetic Region.—The food resources in the limnetic region depend on photosynthesis. Deep lakes are usually plankton-poor lakes, and the depth of the maximum of food resources varies in different types of lakes. Steuer (1910) gives the figures in Table 6, which show comparable catches of plank-

TABLE 6.—PLANKTON AT VARIOUS DEPTHS IN THREE EUROPEAN LAKES Expressed in Cubic Centimeters per Unit of Area

Depth, meters	Plöner See	Luntzer See	Neuenburger See
0–2	76.0	6.1	1
2–5	15.2	44.1	2.8
5–10	15.2	56.2	9.9

ton in three European lakes. In the alpine lake listed in the last column of the table, the greatest quantity of plankton is at depths of 5–10 m., and near the surface there is nothing; in the plains lake (left) there is more near the surface. In lakes the average quantity of available food in each unit of volume generally decreases as the sizes of lakes increase. "The uniformity of the plankton from year to year and from season to season demonstrates the stability of Lake Michigan as a freshwater habitat" (Eddy 1927), but the plankton in small lakes is often subject to great fluctuations (Eddy 1934). The quantity of the net plankton is often far below that of the nannoplankton. In Wisconsin lakes the latter varies from slightly less to fifteen or twenty times as great. "Large amount of plankton is usually associated with much CO_2, little oxygen, and a large amount of dissolved carbonate" (Ward & Whipple 1918). In Green Lake, Juday (1924) found that the dry organic matter from the net plankton varied from 73 to 1,135 and that of the nannoplankton from 795 to 3,151 mg. per cubic meter. In the former, 53 per cent was crude protein, and 12 per cent was extractable by ether; in the latter, crude protein was 43 per cent and ether extract 6.5 per cent. As in other habitats, the quantity of life that may exist depends on the quantity of green plants, and the zone of photosynthesis produces these. Rotifers and crustaceans, which are largely confined to the epilimnion in summer, feed directly on plants. Crustaceans, not plants, are the chief food of fishes like the ciscoes and perch, that feed on plankton. Gulls, terns, fish ducks, trout, and lawyers in turn feed on fishes. In summer, food may be more abundant near the surface, and certain animals may migrate there, but in winter the region near the bottom supports most of them. Plankton continually settles down and mingles with the bottom ooze, which supports a group of animals (chironomids, crustaceans, etc.) that furnish food for many limnetic animals. In Scottish lakes poor years for trout are associated with great growths of algae (Cyanophyceae), which flourish when large amounts of organic materials are washed in from the land during rainy seasons (Rosenberg 1937).

Limnetic Plankton Migrations.—Many plankton animals migrate up and down each day, especially during the summer. In an alpine lake Juday (1907) found no periodic diurnal movements, and Steuer (1910) notes that such movements decrease or

cease in winter. In some cases the extent of migrations is proportional to the amount of light. Young plankton animals move less than adults. Steuer states that peridinians may move downward as much as 2 m. on cold nights. Crustaceans may move 40 m. Most migrants come to the surface at night and descend into deeper water during the day. Not all species, however, reach the surface at the same time. In bright sunlight even young crustaceans desert the upper half meter. Juday (1921) has described the migrations of the phantom larva (*Chaoborus punctipennis*) in Lake Mendota. This insect comes to the surface about 1.25 hours after sunset, and at 10 P.M. as many as 4,730 per square meter were found at the surface. At 4 A.M. all had left the surface, and by half an hour after sunrise the majority were buried in the bottom mud 23 m. below the scene of their midnight foray. Leptodora is a crustacean that makes extensive vertical migrations. In summer most migrants in the epilimnion do not descend below the mesolimnion, and many move only a meter or two.

Association *a*. Animals of Epilimnion

The stratum of photosynthesis and summer warmth supports more life per unit of area than any below it, but large surface invertebrates, like the pteropods, cephalopods, ctenophores, and medusae of the pelagic province of the ocean, are completely lacking. Neither are there any specialized nekton animals comparable to the flying fishes and whales of the open ocean. Crustacea, rotifers, and flagellates make up the bulk of the animal plankton; the nekton fishes are largely salmonoids which not only frequent the open lake but at certain seasons invade littoral or deepwater habitats to feed, breed, or pass the winter. In temperate regions the epilimnion is clearly defined by distinctive temperatures only during summer; in winter many of its plankton animals are rather evenly distributed in a lake from top to bottom. Daphnia and Bosmina in summer migrate up and down in the epilimnion but in winter migrate little and are scattered throughout lakes (Steuer 1910, p. 347). During summer in Lake Mendota black crappie, white bass, and yellow perch feed on plankton and insects throughout the epilimnion, but in winter are found only near shore or in deep water.

Association *b*. Animals of Hypolimnion

In freshwater there is nothing comparable to the fauna of the "twilight zone" of the ocean. Throughout the year there is a stratum where light decreases to little or nothing. In summer there is a well-established mesolimnion where temperature changes rapidly and where oxygen may decrease and carbon dioxide increase. The writer's observations (1920*a*) indicate that fishes do not migrate along the line between warm and cold water or between water that is with or without oxygen, but have

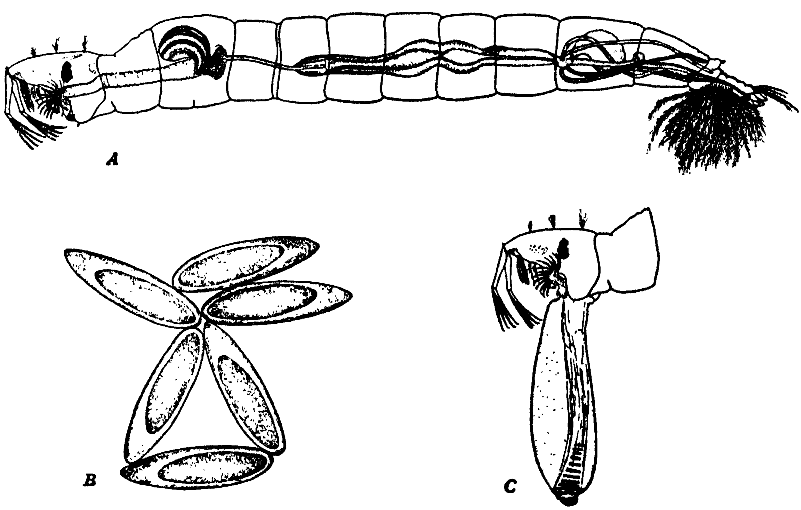


Fig. 96.—Eggs and larva of Chaoborus. *A*, larva; *B*, eggs; *C*, head of larva with pharyngeal feeding basket extended. (*From Herms* 1937.)

relations primarily with the surface, bottom, or shore. The mesolimnion serves as a barrier in the vertical migrations of many animals and is invaded at times by animals that normally live above or below it but has no proper fauna of its own.

The hypolimnion, however, has certain characteristic animals. Juday (1919) has described a ciliate that appears in Lake Mendota each summer when oxygen is used up in the hypolimnion and remains in abundance until the fall overturn:

> There did not seem to be any correlation between the vertical distribution of this ciliate and the temperature of the water or the amount of free carbon dioxide, but there was a definite correlation with lack of dissolved oxygen.

The phantom larva also is found in the hypolimnion in summer. It goes near the surface and by secretion (Akehurst 1922, Damant 1924) fills its air sacs with enough oxygen to allow it to remain for a day or more in the oxygen-free bottom mud. During the summer stagnation season, perch appear to invade the hypolimnion for brief periods in order to feed on bottom organisms (Pearse 1920*a*). There are few or no lake fishes that live in deep, open water without relations with the bottom; no fauna like the bathypelagic of the ocean is present. In lakes that do not stagnate but have a clearly defined hypolimnion, a number of organisms, like *Leptodora, Heterocope, Cyclops strenuus*, etc., live characteristically below the mesolimnion. In Lake Baikal there is a dinoflagellate (*Peridinium baikalense*) which belongs to a group of stenothermic cold-water types, such as Cyclotella and Melosira, and is usually found at depths of 25–50 m. where temperatures are 2–2.5°C. (Kisselew & Zwetkow 1935).

FORMATION 3. BOTTOMS IN DEEP WATER

Benthic Region.—At a depth of 8–10 m. the bottom of a lake changes from the sublittoral to the soft ooze characteristic of deep water. The ooze may vary, but it always contains more or less of both mineral and organic sediments. The oozes in deep water are usually not so productive of animal life as muddy bottoms in littoral habitats, largely due to the absence of light for photosynthesis and the consequent dearth of organic food, but in many lakes stagnation is also a factor in keeping certain animals out of deep water. Shallow lakes in which water circulates freely at all depths and in which light penetrates to the bottom or is an important factor in producing growths that have contact with the bottom, have no truly deepwater habitats and, though their bottoms may consist of oozy mud, are to be classified with littoral habitats. Deepwater deposits are usually not developed in depths of less than about 10 m. and when they are in depths below 50 m. usually have a different fauna from that which is characteristic between 10 and 50 m. Wesenberg-Lund (1905) has described a diatom ooze as being characteristic of cold lakes of moderate depth but lacking in very deep lakes, apparently because it is dissolved. He also describes a black, fetid ooze that forms in shallow lakes from Cyanophyceae and other materials. In small lakes without Cyanophyceae there may be a

chitinous ooze, formed from the shells of Daphnia and other organisms. Alm (1922) names various types of bottoms from the dominant animals that are usually found in them—chironomids, oligochaetes, amphipods, turbellarians, etc. Ekman (1915) in discussing the bottom animals of the Vättern distinguishes those on mineral bottoms from those on chitinous ooze. In Japan many lakes contain much hydrogen sulphide in deep water and are azoic except during circulation periods when insect larvae are present (Miyadi 1931). Yoshimura (1932) has classified Japanese lakes into three types, according to nitrogenous compounds and phosphates present, as polytrophic, mesotrophic, and oligotrophic; but Miyadi (1933) believes that eutrophic lakes are better characterized according to succession in bottom faunas as: (1) oligochete, or Tanytarsus; (2) Tanytarsus-Endochironomus; (3) Plumosus; and (4) Corethra lakes. To the writer the important factors that differentiate different types of bottom habitats appear to be: (1) presence or absence of organic food, (2) variable or low constant temperature, and (3) aeration of water. The less there is of organic food the fewer the animals present. On deep, cool bottoms where there is oxygen, ciscoes, Pontoporeia, and Mysis are characteristic; at moderate depths, even where the water is stagnant, dipterous larvae are typical. Oligochetes, Pisidiums, and some other animals may occur in both situations.

Animals on Deep-lake Bottoms.—Lakes do not have a highly adapted abyssal fauna like that in the ocean, probably because they are geologically too evanescent, but below depths of 10–20 m. certain Sphaeridae, midge larvae, oligochetes, nematodes, and protozoans are usually the dominant animals. Hydras, bryozoans, snails, and mites may also occur. In Lake Erie, Clemens (1922) found millions of hydras (*H. oligactis* Pallas) below the limits of wave action. In deep lakes there are often relicts from glacial times, and some of these have marine affinities—Mysis, Pontoporeia, Chiridotea, etc. Calman (1915) believes that some deepwater animals (Asellus) show relationships to those occurring in ground waters. The smaller bottom animals support predatory fishes like the eel, ling, cottids, and yellow perch.

Vertical Ranges of Benthic Animals.—In Lake Cayuga (depth, 133 m.) Baker (1918) found that molluscs were very scarce below 8 m., and in Lake Nipigon (123 m.) Adamstone

and Harkness (1923) also found that most of the molluscs were restricted to shallow bays, but in Lake Mendota (23 m.) Juday (1922) found an abundance of animals living in the bottom mud. Baker (1918) states that several species of molluscs occur in Georgian Bay at a depth of 37 m., and Ekman (1915) found no significant decrease at greater depths in the Vättern. In Lake Nipigon the numbers of macroscopic bottom animals per square meter were as follows: molluscs, 178; oligochaetes, 87; amphipods, 324; ephemerids, 25; trichopterans, 12; chironomids, 351; total, 1057 (Adamstone 1924). For Lake Mendota, Juday (1922) gives the following average numbers per square meter in the deep water: oligochetes, 3,500; Pisidium, 557; Chironomus, 593; Corethra,[1] 10,830; Protenthes, 185. The dry weights in kilograms per hectare were: oligochetes, 4.6; Pisidium, 2.7; Sialis, 1.8; Chironomus, 22.8; Corethra,[1] 16.0; Tanypus, 1.3; total, 48.2. Nipigon and Mendota may serve as examples of deep and intermediate lakes that are reasonably productive. Zschokke (1901) has given figures relating to the bottom animals in the alpine lakes in Europe; Ekman (1915) has done the same for Swedish lakes.

Depth apparently influences the distribution of certain bottom animals directly and that of others by its influence on other factors. The only molluscs that extend below 25 m. in Lake Michigan are Sphaeridae (Shelford 1915). In Europe, however, there are snails at great depths (Forel 1869). In Lake Michigan, yellow perch and common suckers never descend into deep water, but the long-nosed sucker and blackfin live only in deep water (Pearse 1921). In Lake Nipigon, Clemens (1923) found that the northern sucker lived at lower levels than the common sucker, and the "round" whitefish above the "common" whitefish. In this lake the two regions of greatest productivity are the littoral and profundal zones (Cronk 1932). In Lake Michigan the maximum benthic population is at depths of 40–50 m., where there may be 10,200 animals per square meter, mostly Pontoporeia, Tubificidae, and Shaeriidae (Eggleton 1936, 1937). Some animals (Pontoporeia, Mysis) are never found in shallow water but are most abundant in or near the soft ooze at the bottom of deep lakes. Juday (1924) in Green Lake found the greatest variety of species (39) in the stratum between 1 and 10 m.

[1] Now changed to Chaoborus.

and the least (14) between 44 and 66 m.; the greatest number of individuals occurred between 20 and 40 m., where there were fewest fishes, at least in summer (Pearse 1921). Below a depth of 20 m. there were no Hyalellas, May-fly nymphs, Sialis nymphs, caddis-fly and Orthocladius larvae, or snails. Zschokke (1906) in an alpine lake found that certain animals occurred at greater depths than in those in the lowlands, chironomid larvae being common at 200 m. Birge and Juday (1921) in the Finger Lakes in New York found chironomid larvae at various depths up to 172 m.; at 113 m. in Lake Cayuga there were 3,863 per square meter, far exceeding all other animals in numbers. In these lakes the amphipod Pontoporeia was also abundant, and oligochaetes in half the hauls furnished more than half of the organic material.

In speaking of the bottom organisms of Lake Nipigon, Adamstone (1924) says:

> There are two distinct groups of animals, the one inhabiting largely the shallower water 0 to 30 feet deep, and the other forming the characteristic population of all areas of more than 180 feet deep. The zone between these depths, that is, 30 to 180 feet, is relatively unproductive.

He divides bottom animals into two groups as follows:

Shallow-water Fauna:
- Mollusca:
  - Gastropoda
  - Lamellibranchiata
- Chironomidae
- Ephemerida
- Trichoptera
- Amphipoda
- Nematoda

Deep-water Fauna:
- Amphipoda
- Oligochaeta
- Chironomidae
- Ostracoda
- Mollusca:
  - Lamellibranchiata

In Lake Ontario, Adamstone found that there was a higher percentage of lime in the shallower water, which was, therefore, favorable for the growth of molluscs but that the percentage of organic matter increased with depth, which was believed to account in large measure for the increase in the number of certain bottom animals at greater depths. Certain lakes have been reported which have several separate depressions on their bottoms, and these differ physically, chemically, and biologically (Welch & Eggleton 1935).

Migrations of Benthic Animals.—In lakes where the deep water becomes stagnant for a period between the spring and autumn overturns, some bottom animals migrate into the epilimnion (Limnesia, Sialis, Perca, Leuchthys) and remain, but others (Chaoborus) swim up each day and secure a supply of oxygen. Chaoborus larvae escape from predaceous fishes by remaining buried in the bottom mud during the day. In Lake Mendota 16 genera of protozoans, many oligochetes, nematodes, gastrotrichs, rotifers, an ostracod, a Cyclops, midge larvae, and a Pisidium each year remain for 3 months on or in the bottom mud in water that contains no oxygen. The Cyclops is inclosed in a cocoon; the ostracod and the clam remain with the valves tightly closed; the oligochetes, chironomid larvae, and protozoans remain more or less active (Birge & Juday 1911). In Lake Nipissing, ciscoes leave the warming epilimnion in spring and remain in the hypolimnion until autumn (Fry 1937). Apparently temperature and food are the most significant factors in such migrations.

Food of Benthic Animals.—The food of bottom-dwelling Sphaeridae, amphipods, oligochetes, and midge larvae consists largely of organic ooze. The protozoans consume bacteria and other minute organic particles. The bottom fishes for the most part feed on plankton as well as bottom organisms and ooze. The yellow perch may feed at times at the surface or among water plants and at times grub about in the ooze. The ciscoes eat mostly Mysis, Pontoporeia, entomostracans, and small fishes. The whitefishes prefer insect larvae, molluscs, and fishes. The cottids prey on amphipods and schizopods. The ling and trout catch insects and fishes. Suckers are the only fishes that consume ostracods and mud in considerable amounts. Juday (1924) says of Green Lake:

> Considering the entire lake, the dry organic matter in the average standing crop of total plankton was ten times as large as the dry weight of the total bottom population [littoral and deep water], but the organic matter of the average crop of plankton, rotifers, and Crustacea amounted to only one-fifth of the dry weight of the bottom population.

Moore (1922) in speaking of the plants of Lake George stresses the importance of algae that grow at depths of 6–15 m. as food and shelter for young trout and other fishes.

With the exception of Chaoborus larvae, bottom-dwelling invertebrates are small and weak and, though they usually burrow, in some cases swim feebly. Food settles continually from above, and hiding is easy on account of the absence of light and the presence of the soft mud. At times lack of oxygen or unusual amounts of sediment may suffocate bottom animals, but they are generally able to escape such dangers. Except for Chaoborus larvae, few of the animals require contact with aerated water, and many are able to spend long periods without oxygen. Most of the bottom animals are dull in color, and a few have degenerate eyes. Most of the fishes that frequent the bottoms in deep water are also found at higher levels, but there are a few (ling, cottids, etc.) that are not.

Association *a*. Bottoms of Moderately Deep Lakes Having Variable Bottom Temperatures

Midge larvae, chironomids, Sphaeridae, ostracods, and protozoans are typical animals on or in the bottoms of lakes (Fasciation 1) having depths up to 25 m. Above the bottom (Fasciation 2) swim such fishes as yellow perch and suckers, which feed more or less on the mud-dwelling invertebrates. There are also certain pelagic animals (Leptodora, Limnocalanus) that rest near the bottom, especially during the day.

Association *b*. Bottoms of Deep, Cool Lakes

Below 25 m., lakes with increasing depth contain more of the relicts, Pontoporeia and Mysis, and fewer midge larvae. Ostracods and clams may be abundant, and in some European lakes there are snails, isopods, and mites. Typical fishes are lings, cottids, ciscoes, and eels. Lake Baikal is remarkable for the abundance of its bottom animals, which even at depths of 200 m. average 170 kg. per hectare (Miklashevskaia 1935).

Saline Lakes

Biota in Salt Lakes.—Inland lakes without outlets sometimes become very salty, but a few salt-tolerant plants and animals persist in them. Among these the phyllopod crustacean known as the brine shrimp, *Artemia salina*, is famous. It lives and breeds in very dense salt solutions and is often found in the shallow ponds where water is evaporated to obtain salt. Certain

dipterous larvae (Ephydra, Aedes, etc.) also have unusual toleration for salt and flourish in very concentrated solutions, which have salinities more than twice that of sea water. In Great Salt Lake, Utah, Vorhies and Daines (1917) recorded four to six species of algae and five of bacteria, Artemia, Ephydra larvae, and water boatmen. Ping (1921) made a careful study of all stages of *Ephydra subopaca* in salt pools near Ithaca, N. Y. It lives in salinities as high as 9.7 per cent in pools with algae and Protozoa. In salt waters near Calcutta, Seymour-Sewell (1934) found several species of freshwater copepods which occurred in saline waters. In Devils Lake, N. D., Edmondson (1920) found a dearth of shelled rhizopods but representatives of other groups of freshwater protozoans in salinity of about 1.0 per cent.

Subprovince B(b). Ponds

Character of Ponds and Biota.—There is, of course, a gradual transition from lakes to ponds, and a small lake has general characteristics and an animal population more or less like those of a pond. The shallowness and the limited area make the effects of wave action slight, and floating or emergent vegetation reduces such motion still more. In ponds there are no limnetic or deepwater formations. Svec (1897) studied the infusorians in ponds and found seven pelagic, 69 littoral, and few individuals of six bottom species. The littoral region of a lake shows a great variety of habitats, but a pond is usually rather monotonous. Ponds may differ greatly from one another, however. Scott (1910) has made it clear that inland ponds are colonized accidentally by plants and animals which enter soon after the ponds are formed. The first immigrants to arrive, having no competition, soon spread and dominate the pond, giving it its particular "character." Shelford (1913) has pointed out that aquatic vegetation is characteristic of older ponds and that bare, sandy bottom is usually found only in young ponds. Reed (1901) found the following vegetation zones in Michigan ponds: (1) Characeae, (2) Potamogeton, (3) Nymphaea, (4) Carex and Sphagnum, (5) Salix and Populus, (6) Gramineae and Compositae. In general, the types of plants mentioned are arranged in the order of their succession in ponds. In youth, a pond may support patches of stoneworts

on its clean bottom; as sediments accumulate and adolescence approaches, submerged and floating plants increase; at maturity, sedges and other emergent plants begin to invade the pond from its margins; in old age, land plants gain a foothold, and gradually the pond is converted into a terrestrial habitat. The usual succession of ponds is from bare bottom to vegetation-covered bottom, to swamp, to land. As a pond grows older its animal life increases in quantity, and, with poorer aeration and more putrefaction, there is an increase in the proportion of types that depend more on the atmosphere than on the water for respiration.

Fischer (1924) has made careful studies of the amounts of phosphorus, potassium, and nitrogen compounds in fishponds in Europe. He finds that nitrogenous compounds are usually not removed but are deposited in ponds and that nitrogen-fixing organisms are usually present in considerable numbers. In general, fishes increase or decrease as phosphorus increases and decreases. Fischer concludes that phosphorus compounds and nitrogen-fixing bacteria are the chief limiting factors in the production of animal life, particularly fishes, in ponds.

FORMATION 1. LITTORAL REGIONS

All animals in ponds occur in habitats that resemble the littoral regions of lakes, and most of the plants and animals are the same in the two situations. Ponds differ from lakes, however, in the absence of limnetic species which at times invade littoral lake habitats.

Association *a*. Ponds with Bare Bottoms

Young ponds are populated by species of mussels, snails, immature insects, and fishes that may also occur in lakes and rivers. The fishes are those that require well-aerated water for respiration or bare bottom for breeding (Shelford 1911*c*). The shores have the usual animals associated with the margins of bodies of water. The water itself contains some plankton organisms. The population, however, is usually, on the whole, rather scanty. In older ponds bare bottoms often persist when water is so deep that plankton and other materials decrease transparency so that plants do not obtain a foothold on muddy bottoms. Such ponds usually contain an abundance of plankton, fishes, turtles, and other organisms, unless the water is

strongly acid in reaction. In temperate regions temperatures are high in summer and cold in winter. Among copepod plankters Cyclops is more characteristic than Diaptomus (Tressler & Domogalla 1931). In two quarry ponds in Wisconsin that had a maximum depth of 5 m., plankters, except crustaceans, were most abundant in the upper meter (Wimmer 1929). Alm (1922) has made a quantitative study of a pond in Sweden and discusses the relations of European pond faunas. In a pond only 2 m. deep Weimann (1933) found a stratification of plankton. In sinkhole ponds in southern Illinois plankton consists of few species and is rather uniform (Eddy 1931). In a bog pond in Massachusetts a holozoic protozoan, *Gonyostomum semen*, carried on diurnal migrations and produced rhythmical changes in oxygen and carbon dioxide (Cowles & Brambel 1936). Newts (Triturus) resort to older ponds to breed and show a considerable degree of discriminative ability in selecting such as are favorable for the development of their tadpoles (Hudson 1930).

Association *b*. Animals of Ponds Containing Vegetation

Old ponds usually support an abundant plant and animal population. On the beaches above the water (Fasciation 1), spiders, toads, frogs, and many terrestrial animals are to be found. On the surface of the water (Fasciation 2), bugs and beetles seek food, and many from below (mosquito larvae, back swimmers, Scapholeberis, etc.) commonly hang from the surface film. Ducks, grebes, and other birds are also attracted to ponds by vegetation and the animals associated with it. Along the shore line (Fasciation 3) many insects and other animals resort. Adams (1909) noted that aquatic beetles were more abundant near the margins than toward the center; Needham and Williamson (1907) showed that the size of beetles is graded according to the distance from shore, the larger species being farther out in the water. The vegetation (Fasciation 4) in ponds supports a large animal population. Immature and adult insects, snails, clams (Sphaeridae), leeches, rotifers, entomostracans, amphipods, oligochetes, nematodes, and protozoans climb about on plants. Among the stems and leaves lurk shrimps, crayfishes, bullheads, mud minnows, breams, and crappies. Attached to the aquatic plants are midge larvae, bryozoans, hydras, worms, rotifers, and protozoans. Among the plants, turtles, muskrats, and fishes

move about, seeking food and shelter. There are also many microscopic animals (entomostracans, mites, rotifers, protozoans) that swim about in the water of ponds (Fasciation 5). Not many animals are associated with the bottom (Fasciation 6), and some of those that are (rat-tailed larva) have special adaptations for securing air from the surface.

Subprovince B(c). Swamps, Bogs, and Pools

In swamps, bogs, and pools the amount of water varies greatly, and at certain seasons water above the soil may be absent altogether. There is often a general relation between the sizes of animals and the volume of the water in which they live; some species grow larger in large bodies of water, and some large animals are not present in small bodies. The season of failing water may also directly influence the life cycles of animals. Metamorphoses may be shortened by lack of water; encystment or estivation may be brought about by changes in the level or content of water.

FORMATION 1. SWAMPS AND BOGS

Swamps and bogs are usually surrounded by zones of vegetation, which grow more mesophytic and less hydrophytic at higher levels. Swamps are shallow and especially characterized by the presence of emergent vegetation with submerged roots. There is shelter above the surface of the water. Bogs have vegetation, like Sphagnum, which covers part of the surface of the water and the surrounding soil. Sphagnum has remarkable ability to hold water and in some cases makes "climbing bogs" by growing up inclines. The floating plants in bogs and swamps are not the same as the plankton plants of lakes but largely megaphytes, like Lemna and Ceratophyllum. Even the algae are not those species characteristic of lakes. Swamp plants are largely perennials; but where a whole area dries up, there may be a preponderance of annuals. Adventitious roots and runners are common, and many plants migrate by vegetative propagation. Some plants have two forms of leaves which appear above or below the water.

The animal population of bogs and swamps may be dense but usually presents little variety. There is a more or less definite zonation of certain animals in relation to the shore and stratifica-

tion with reference to submerged and emergent vegetation. The extreme and sudden variations in temperature and the shallowness keep out limnetic species.

Association *a*. Swamps

The animal population of swamps may vary greatly at different seasons on account of fluctuations in the height of the water.

Fasciation 1. Emergent Vegetation.—The emergent vegetation of swamps is a favorite resort of many birds—rails, bitterns, herons, coots, grebes, swamp sparrows, marsh wrens, blackbirds, bearded titmouse, etc. Most of these find food among the aquatic vegetation. There are also predaceous birds (marsh hawk, short-eared owl) that live about the margins of swamps and hunt among the plants. Marsh wrens defend breeding areas in swamps. They build dummy nests and seek for food among the emergent vegetation (Welter 1935). Swamp rabbits are able to swim and run through soft mud. They do not jump like species that live on land (Tomkins 1935). In winter, meadow voles come in from surrounding terrestrial habitats and live on the ice among the matted vegetation. Muskrats at all seasons find food and shelter in swamps. Most of the invertebrates live on or below the surface of the water throughout most of the year, but in summer there are often many adult insects and emerging nymphs above the water. Amphibious snails also crawl about. Certain spiders (Tetragnatha, etc.) are commonly found. At the margins of swamps there are a number of hangers-on which may live on land or spread out into the swamps on the emergent vegetation. Certain grasshoppers, slugs, frogs, and snakes commonly frequent such situations.

Fasciation 2. Surface of Water.—On the surface of the water are water striders, whirligig beetles, bugs, and spiders. With these are associated frogs and other small animals which hop over the surface of the floating vegetation.

Fasciation 3. Submerged Vegetation.—In the submerged vegetation are protozoans, rotifers, nematodes, water bugs and beetles, insect larvae and nymphs (dragonflies, mosquitoes), ostracods, amphipods, isopods, snails, Sphaeridae, mud minnows, bullheads, and turtles. Needham and Williamson (1907) found that dytiscids were largely confined to the cattail zone; also that

the largest and strongest swimmers ranged farthest from shore. Some animals (Hydra, entomostracans, etc.) that live among the vegetation frequently hang from the surface film (Scourfield 1911).

Fasciation 4. Swamp Water.—The standing water in swamps supports little life that is peculiar. Many of the small animals that swim about are associated primarily with vegetation. Temporary pools in swampy areas are invaded quickly by aquatic insects, especially bugs, beetles, and dragonflies (Carter & Beadle 1931, Pearse 1932*b*).

Fasciation 5. Bottom Animals.—The bottom animals are few in swamps at time of high water, but in time of drought the bottom muck may serve as a refuge for estivating insects, snails, and other animals. The vegetation becoming matted over the bottom also helps to conserve moisture, and animals may survive dry periods beneath it. Certain fishes that frequent swamps are able to live for a time in soft mud or for longer periods in a torpid condition within cocoons of slime and mud (Pearse 1936, Vellard 1934).

Desiccation of Swamp Animals.—Desiccation is a common experience for most swamp animals, and many of them are able to become encysted or assume other resting states. Rotifers, tardigrades, and nematodes can readily survive drying (Baumann 1922). Mrázek (1913) reported an oligochete that multiplied within a cyst wall when dried. Frierson (1899) states that a clam, *Unio declivis* Lea, can live for 9 months in dry mud without free water. Mud minnows can remain buried in mud for some time and when a swamp dries up completely may migrate to water by wiggling over the land (Gill 1903). Lepidosiren, when a swamp dries up, burrows into the deepest part, shoves a clay plug up to close itself in, curls its tail over its nose, and remains alive in a slime and mud "cocoon" for months. The eggs of snails, like Limnaea and Aplexa (Baker 1914) remain alive in dry mud at the bottoms of swamp pools. The winter eggs of swamp cladocerans stand drying (Morgan 1907).

Effects of Stagnation and Decay of Organic Materials.—Swamps, on account of their shallowness, great amount of organic matter, and lack of water circulation, are often quite foul and may at times have little oxygen in their aquatic habitats. Under such conditions some chloryphyll-bearing organisms, such as

Euglena and certain infusorians, may flourish. The lack of well-aerated water, however, is doubtless associated with the fact that the majority of swamp animals are air breathers. Lack of oxygen may also hasten the metamorphosis of swamp animals (Morgan 1907). Where large amounts of carbon dioxide and other substances are present, acidity may be an important factor. Warming (1909) states that reed swamps are characteristic of stagnant or acid water. Jewell (1923) found no Cyprinidae or



FIG. 97.—Eggs of a snail deposited above the plant-covered surface of a swamp, where they escape enemies and are not immersed in water that lacks oxygen, Colombia.

molluscs in a swampy lake having a pH of 4.4 with abundant oxygen, but certain fishes (perch, bullhead, pickerel) were abundant. In many swamps decay is largely inhibited by acidity, and peat accumulates. Tropical fishes that live in swampy areas commonly breathe air or respire close to the surface. Air-breathing vertebrates probably originated as a result of living in poorly aerated water, rather than from the effects of aridity on land (Carter & Beadle 1931, Hora 1935, Pearse 1936).

Reproduction in Swamps.—The conditions in swamps in many ways influence the reproductive activities of swamp animals. The decay of rubbish may maintain a high temperature even during cold seasons, and animals that resort to swamps may be able to breed earlier or for longer periods than those in other habitats. Morgan (1907) points out that certain swamp cladocerans have two periods of sexual activity—in July and October. The "winter" eggs of these crustaceans can stand drying and may be produced more than once a year. Kennedy (1907) says that the swamp species of odonates in the genera Lestes and Sympetrum are adapted in various ways. Only one brood is produced each year; eggs winter over and hatch with the beginning of spring rains. In temperate regions swamps often afford the earliest open water and in spring furnish more or less warm, protected situations. Amphibians use them for the deposition of their eggs. When the hot stagnation of midsummer comes, most of the tadpoles have turned largely to air breathing, and some have become wholly terrestrial. The exact situations where frogs' eggs are deposited are, according to Wright (1921), nicely adjusted to various conditions. Some eggs are deposited singly, others in great masses; eggs may float, adhere to sticks, sink to the bottom, etc. Turner and Bahr (1907) have given an interesting account of the breeding of birds in swamps. Decaying plants keep the grebe's eggs warm, and the male continually dives for dead rushes which he heaps up over the nest. The rail draws the tips of rushes together over its nest. During rains a male snipe assists his mate with the brooding.

Annual Succession in Swamps.—Peterson (1924) has studied seasonal succession in a swamp near Chicago.

> The succession in the pond, in general order of appearance, in spring was Crustacea, gilled snails, pulmonate snails, insect nymphs, larvae, and adults. . . . The data indicate that the general seasonal succession of animals is caused by temperature-water level conditions, and that pH and oxygen tension are accompanying rather than causal factors.

In winter, swamps are a refuge for many hibernating frogs, turtles, aquatic insects, and other animals. Some of these spread into terrestrial habitats during warmer seasons. In the bottom mud they may be very cold during the winter, but an animal with some salts in its body to lower its freezing point below

that of water will not actually solidify and hence generally survives. While in a torpid condition, hibernators are concealed from predaceous enemies by mud.

Association b. Bogs

Bogs resemble swamps but are generally shallower. Their surface vegetation may float on water but usually rests on a

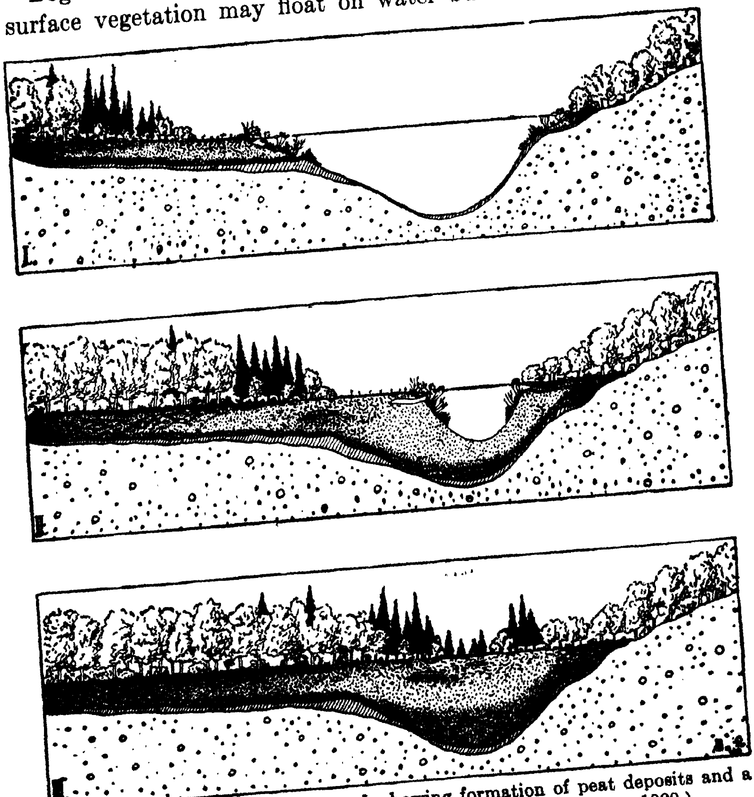


FIG. 98.—Succession in a bog pond, showing formation of peat deposits and a climax forest. (*After Dachnowski, from Weaver & Clements* 1929.)

substratum of soft, quaking mud. Sphagnum bogs often inclose pools; and about the margins of these, sphagnum moss, assisted by other plants, forms mats which extend out some distance over the water. Bog plants have been much studied by botanists, but the fauna has been little investigated, except in connection with other problems. Dachnowski (1912) has perhaps given the most

extensive survey of the bog-plant societies. Leaf decay is commonly suspended in bogs on account of acidity, lack of oxygen, and low temperature, and peat deposits are therefore characteristic. Bog deposits are often deficient in potassium and available nitrogen (Transeau 1905). Some of the emergent vegetation (pitcher plant, etc.) has special means for securing nitrogen through animal food. Animal life is, as a rule, rather scanty in bogs, and Dachnowski (1905) has shown that bog water is toxic for a number of species. It has been commonly supposed that bogs are characteristic of cool climates (Transeau 1903), but Bird (1923) maintains that bog plants depend on acidity more than temperature and that the insects present are largely associated with particular plants. Needham and Lloyd (1916) state that, in their opinion, plants are eaten less by animals in bogs than in other situations.

Certain insects and snails that frequent the margins of swamps are also found along bogs among the sedges and other emergent vegetation. There are also some, like those that live in pitcher plants, that are not found elsewhere. Frogs, birds (heron, bittern, etc.), and muskrats hunt about over the surface vegetation. On the surface of the pools there may be a few podurans and water striders. The water contains few animals, except Sphaeridae, certain beetles, and a few microscopic species. Bottom animals are usually wholly or nearly absent (Welch 1936). Chaoborus larvae persist and are often found when other insects are unable to live (Ueno 1934). They rise to surface waters at intervals to breathe.

FORMATION 2. POOLS

Pools are like swamps in being shallow and of small size, so that the water varies greatly in amount and usually dries up completely at certain seasons, but are unlike them in lacking characteristic vegetation. They are either without plants or possess a vegetation that belongs properly to land. Animals living in pools are usually subjected to wide variations in temperature and must be hardy. Steuer (1910) states that pool plankton is primarily animal and that it consists largely of crustaceans. Pools are formed after periods of rain and for a time serve as refuges, feeding grounds, or breeding places for various animals.

Some of the animals die when a pool dries up; some migrate to other aquatic habitats; and some enter into a resting condition.

Association *a*. Pools with Hard Bottoms

Animals that live in pools in smooth rocky basins, in tanks, water troughs, and similar situations usually have good powers of migration, but, if there is a little sediment present, they may be able to survive dry periods. Zacharias (1906) gave a list of algae, protozoans, rotifers, and nematodes that he found in a large stone urn. In pools there may be such insects as water bugs and beetles which remain for a time and then fly elsewhere. Because of the dearth of organic food there will rarely be an abundant growth of plankton, but algae may flourish and support such organisms as isopods, amphipods, and entomostracans. These may be introduced on the bodies of wandering animals like ducks and snipe.

Association *b*. Pools with Muddy Bottoms

In pools where there is an accumulation of sediment over the bottom many animals are able to exist that are not present in pools with smooth, hard bottoms. Scott (1910) studied a pool in a limestone basin in Indiana and gives lists of the plants and animals. There was little plankton in January and February, but in summer considerable numbers of active protozoans, rotifers, cyclopia, and cladocerans occurred. Ostracods and difflugias were common. The former were important agents in comminuting the dead plants, and beetles also helped by knocking the plants to pieces. The annual range of temperature was from 0–27.8°C., and animals were generally active when it was above 4°C. On Oct. 12 there was a change of 10° in 24 hours. In a meadow pool in Europe, Sekera (1907) found cosmopolitan animals which included rhizopods, infusorians, planarians, and crustaceans. In Bohemia, Mrázek (1913) found an oligochete that was associated with Apus and Branchipus in pools that dried up. Perhaps phyllopod crustaceans and certain rotifers are as characteristic of pools as any animals. Shelford (1918) studied the succession of animals in a pool in Illinois. About Mar. 15 Ambystomas were depositing eggs; a month later Eubranchipus was common; May 1, *Planaria velata* and *Diapto-*

mus stagnalis were the dominant species. Temporary pools are often invaded by aquatic insects (Squire 1936).

Adjustments to Desiccation in Pool Animals.—The animals of pools are usually adjusted to drought and wide variations in temperature. When a pool dries up, many of them become encysted, burrow, or migrate. Some have a brief life cycle



Fig. 99.—A tree frog's eggs which were fastened to the base of a bromeliad leaf in the rain water that had accumulated there, Colombia.

and are able to multiply rapidly. There are some that get into pools by chance from other aquatic habitats, but there is also a group that is characteristic. G. O. Sars has described many new species of crustaceans that he has hatched out of dry mud sent from far countries. The eggs of a number of phyllopods are known to be unable to hatch unless they are dried for a time (Herrot 1917). Shelford (1918) states that the salamander, *Ambystoma tigrinum*, "deposits its eggs and then burrows into

the mud and remains 10 months in estivation and hibernation." The writer has taken living mermithids, snails, and Sphaeridae from the sediment in the dry bottoms of pool basins. The eggs of Estheria will develop after being dried for 9 years (Calman 1911).

Phytotelmata.—Ephiphytic waters, or phytotelmata, are classified by Thienemann (1934) as:

I. Fluids at least in part of plant origin.
   1. With digestive secretions (Nepenthes, etc.).
   2. Nondigestive secretions (Zingiberaceae; Commelina).
II. Fluids primarily composed of rain water.
   1. In chlorophyll-bearing parts of plants, as in leaf bases
   2. In nonchlorophyll-bearing parts of plants, as in flowers, bamboo tops, holes in tree trunks, etc.

Such limited and temporary bodies of water are often inhabited by various animals. Some tree frogs (Fig. 99) and mosquitoes regularly breed in such situations, often at considerable distances above the surface of the earth.

PROVINCES C, D. CAVES

Cave Animals.—The population of caves is always scanty, and most of the animals found there are also epigean. There are always less life in the water and less of breeding activities than in comparable habitats in the world above. Certain species of salamanders, fishes, crayfishes, isopods, and insects are wholly confined to caves. The animals of any particular habitat usually show relationships to the local epigean fauna. In general, there is an unusual development of tactile sense organs, and more or less degeneration of pigment and visual organs in long-established cave species. Many transient or accidental visitors to caves are well suited to cave life by their habits. The marine relatives of blind cave fishes have very small eyes and commonly live in holes among rocks. The young of certain cave animals are more sensitive to light than adults. Most of the leeches, rotifers, turbellarians, nematodes, hydras, sponges, and protozoans that have been reported as occurring in caves do not differ from species that are epigean. Scott (1909) studied the plankton of a cave and concluded that it was all epigean. Kofoid (1900) made similar studies, noting a dearth of algae and preponderance of copepods.

Food in Caves.—The food of cave animals must all come ultimately from the outside, as photosynthesis requires light. It is derived from organic remains washed in by water, the excreta and other materials brought in by visitors, and the fungi and other organisms that develop in darkness. Racovitza (1907) states that inanition is the usual state of many cave animals on account of the general scarcity of food. Banta (1907) also stresses the scantiness and irregularity of food resources. The temperature of caves is usually extremely constant at all seasons, and aquatic cave animals usually do not show marked hibernating periods. Habitual rhythms of rest and activity may persist in animals that invaded caves rather recently. In general, there are the most animals where there are the most loose stones or other materials that give shelter and opportunity for the accumulation of food. Eigenmann (1909) points out that smaller caves usually have richer faunas because the animals are closer to the food resources outside. Bats are important sources of food for many small cave animals. They fly out frequently and bring in fruits; their feces contain blood or the remains of plants or animals that furnish foods directly or serve as nutritive media for fungi (Pearse 1938).

PROVINCE E. GROUND WATERS

In subterranean reservoirs and streams there are a few animals. These sometimes appear in caves, wells, and even in the depths of lakes. Calman (1911) says:

> A very remarkable feature of the subterranean fauna is that a number of animals appear to be more closely allied to marine species than to any known from freshwaters aboveground.

This is said to be especially true of certain isopods.

In subterranean habitats, as in caves, light is absent, temperature is uniform at all seasons, and food must come down from near the surface. Animals are commonly like those in caverns—pigmentless, blind, and unusually sensitive to touch stimuli. Salisbury (1919) estimates the average annual rainfall over the whole earth as about 40 in., and rivers carry only about half of this away. The remainder disappears through sinks, pools, soil, evaporation, etc. The surface of the earth is the source of ground water, which probably does not descend more than 1,000 ft. and is more or less continually moving on account of the unequal distribution of rainfall and losses from wells, springs, etc.

CHAPTER X

TERRESTRIAL HABITATS

Land animals that live on or above the surface of the soil are usually subjected to more or less sudden and extreme variations in water and temperature. They also experience periodic fluctuations in light and other environmental factors that change with day and night. Subterranean animals live in conditions that approach those in aquatic habitats, for they are seldom exposed to sudden changes in temperature and are in little danger of desiccation. On land, food resources are, on the whole, more limited and precarious than in water. Plants are often supplied with nourishment slowly or intermittently, in some cases only after rains, and growth is often arrested by drought or cold. The atmosphere, being a medium of low density and high oxygen content, is favorable for locomotion and rapid metabolism.

Zones in Relation to Climate.—Different areas may differ markedly in climate on account of characteristic differences in temperature (maximum, minimum, average of coldest or warmest season, length and temperature of cold or warm season, etc.), available water (rainfall, humidity, evaporation rate, soil, moisture, etc.), winds, intensity and duration of light, soil, topography, altitude, prevailing types of vegetation, and other factors. Most large areas of land are divided into climatic zones, which are related more or less to latitude, altitude, or contiguity to areas of water. Merriam (1898) divided North America into the following zones:

Boreal:
1. Arctic-alpine—snow bunting, musk ox, lemming, etc.
2. Hudsonian—wolverine, moose, mountain goat, etc.
3. Canadian—lynx, marten, porcupine, etc.
4. Transition—fauna varying with humidity.

Austral:
5. Upper Austral—opossum, cardinal, burrowing owl, etc.
6. Lower Austral—mocking bird, road runner, etc.

Tropical:
7. Tropical—jaguar, armadillo, etc.

Dice (1923, 1923*a*, 1923*b*, 1932) has attempted a somewhat more intensive classification and points out that:

> The life zones of Merriam are founded on the belief that there are zones of life extending transversely across the continent of North America, in the south as well as in the north. . . . I have previously pointed out that, although belts of life do occur in the northern part of North America and on mountains, yet the recognition of transcontinental zones of life in the southern part of the United States seems contrary to the facts of distribution. . . . The greatest usefulness of the life zones proposed by Merriam should lie, not in their use for the statement or classification of animal and plant distribution, but in the explanation which they may give as to the factors limiting distribution.

Dice (1922) suggests the use of the term "biotic area" to describe the regions where a group of plants or animals has a more or less common geographic range and shows a general agreement in ranges of toleration to variations in environmental factors. Dahl (1921) has also stressed the fact that the distribution of many terrestrial animals in Europe and Asia is not zonal but often depends largely on local variations in environment and is therefore quite discontinuous. He classifies the mammals of each continent primarily by their food habits and shows that when so assorted they fall into rather definite groups which occur in particular areas.

Vertical Zones.—The relations of animals in their vertical distribution with reference to the surface of the earth are somewhat more definite than their horizontal distribution in particular geographic areas. Flattely and Walton (1922) divide animals into two great groups: (1) phanerozoic, above the soil, and (2) cryptozoic, subterranean or living in more or less complete darkness. Shelford (1912, 1913) also makes a primary division of animals into (1) those exposed to the atmosphere and (2) those out of direct contact with the atmosphere in soil, wood, tissues of living plants or animals, etc. Above the ground, animals may (1) be associated with surface, (2) frequent the vegetation above, or (3) use the atmosphere itself as a highway. A field cricket is usually active on the surface of the ground; a tree cricket lives in the vegetation above; and a condor spends most of its working hours high in the air. In this book, land animals are considered in relation to the following habitats: subterranean, cave, surfaces

of soils of various water contents and slopes, grass, herb, shrub, tree, and aerial. Thompson (1922) points out that the air has been the last nonaquatic habitat to be invaded by animals; that those that live in it are independent of contact with solid objects and are able to avoid dangers and unfavorable environmental changes by migrating across areas that are impassable for other animals. Land plants, with their opportunity to take advantage of radiant energy, produce concentrated foods in the form of seeds and fruits which are rich in essential organic substances. They manufacture starches, oils, and proteins during periods of activity and store these away. Animals take advantage of such stores—beetles bore through the phloem of trees for starch; squirrels hide nuts for use in winter; vegetarian animals feed on leaves; etc. Land plants furnish better supplies of body-building and energy-supplying substances than those in aquatic habitats.

Land Plants as Sources of Food.—Land plants constitute the fundamental food resources for animal life. They differ from those in aquatic habitats in possessing special mechanisms which control the loss and increase the intake of water. Some of them are even able to store considerable water. Many land plants attain great size and are thus able better to withstand cold, heat, and drought. Birds, as examples of land animals, are adjusted to different levels above the ground in remarkable ways; nests, songs, coloration, and other adaptations fit them for particular situations (Linsdale 1938). In a spruce-fir forest in Wyoming, Fichter (1939) found arthropods stratified from soil surface to higher levels, chiefly with reference to humidity.

Water Loss by Land Animals.—Land animals are commonly adapted to retain water or to be able to renew their supply continually. Their coverings are often such as to retard or prevent desiccation and are rigid enough to prevent injury from falls and moving objects. Living in a gaseous medium, land animals can move with less effort than their aquatic relatives and are, on the whole, swifter. Certain of their sense organs (eyes) are also commonly more acute. Respiration in all animals takes place through moist membranes; land animals must breathe and at the same time maintain their water content at a high enough level so that they will not die. Probably on this account there is a general tendency to carry on respiration in internal cavities where there is little loss.

Density of Terrestrial Animal Population.—On the whole, the animal population of the land is scantier than that in the ocean or freshwater. Above ground there are no long stretches that teem with life, like the pelagic and limnetic regions of seas and lakes, and there are many barren deserts. Yet McAtee (1907) estimated that a forest floor contained about 1,216,880 living and dead animals per acre, and a meadow about 13,654,710. In a vacant city lot in Illinois, Wolcott (1918) found an average of 4,500,000 animals per acre, the commonest types being earthworms, sowbugs, beetles, and ants. Darwin (1881) estimated that there were 26,886 earthworms per acre in his pasture. Forbes and Gross (1922) found summer birds in various habitats in Illinois in the following numbers per square mile: stubble, 324; waste and fallow fields, 716; orchards, 1,987. When placed in the order of the number of birds present, various habitats ranked as follows: orchards, yards and gardens, swamps, woods, pastures, shrubs, meadows, waste and fallow lands, cereal crops, plowed fields, cornfields, oat fields, stubble fields. More than five times as many birds occurred in areas covered by trees and shrubs as in those which bore cereal crops.

Origin of Land Animals.—Paleontological evidence indicates that marine animals existed long before there were any on land and that land animals have been derived from those that lived in the ocean and freshwater. At the present time certain fishes, crustaceans, snails, and worms are in the midst of transition from aquatic to terrestrial life. There are various views held as to the causes for the migration of animals to land habitats. Hesse (1913) has emphasized the fact that there is an average of only 7.0 cc. of dissolved oxygen per liter in water, whereas the atmosphere contains 207 cc. He believes that the lure of oxygen has attracted animals to land habitats in moist climates where there is little danger of desiccation. Semper (1881) believed that animals invaded the land for food and shelter. He pointed out that a respiratory organ suited to water breathing would generally function in air if kept moist and prevented from collapsing. Heilprin (1887) and Flattely (1921) attached much importance to tidal action in the origin of land life, supporting the view that animals that were intermittently exposed to the desiccating action of the atmosphere in the intertidal zone gradually became adjusted to life on land. Woodworth (1894) and Barrell (1916) maintained

that land vertebrates arose on account of periodic aridity which forced them to become adjusted to respiration in air; but Case (1926), Harms (1935), Hora (1935), Pearse (1936, 1936*a*), and Raben (1934) believe that land animals more often developed in stagnant water where lack of oxygen forced them to breathe air and that the acquisition of that ability gave them opportunity to invade land habitats.

Routes of Emigration to Land.—Some land animals have apparently been derived directly from the ocean, without first being adjusted to life in freshwater. The ghost crab (Ocypode) goes to the ocean at intervals to moisten its gills and can live only 24 hours without water (Cowles 1908). It lives only 2 hours in freshwater (Gardiner 1903). The sand hopper (Orchestia) lives on land near the ocean but cannot endure freshwater (King 1914). Certain crabs (Birgus, Geacarcinus) live most of their lives far from water but return to the ocean for a few days each year to allow their young to hatch. On the other hand, many animals probably first emigrated from the ocean into freshwater and later became adjusted to land life. Though amphibians were probably derived remotely from marine, fishlike ancestors, they now show little affinity for the ocean (in fact, most species cannot endure salt water), yet many of them have become true terrestrial animals, and a few never visit the water, even depositing their eggs on land. Thompson (1922) states that, though preceded by plants, animals have made three great land invasions: (1) the worms, which largely remained within the soil; (2) the air-breathing arthropods, which generally developed tracheae for breathing; and (3) the vertebrates, which developed internal lungs and toes at the distal ends of their limbs. The snails are also moving to the land at the present time, and some have become completely terrestrial. Their slimy coatings and shells protect them from desiccation and make such migration comparatively easy. Tadpoles that start their development in water and later take up life on land are recapitulating their phylogeny. They first breathe through gills and later turn to buccopharyngeal, dermal, and pulmonary respiration. The land animals came from aquatic ancestors, and certain aquatic animals now make brief journeys on land to escape unfavorable conditions or to acquire some desideratum. They are apparently

able to do this without much trouble as long as their respiratory membranes can function in the atmosphere.

PROVINCE A. SUBTERRANEAN HABITATS

Animals that live underground, either in soil or in caves, are in little danger from desiccation and are less exposed to rapid and extreme temperature changes than those that live above. They may be at times insufficiently supplied with oxygen and may be obliged to come in contact with injurious substances that are present as gases, liquids, or solids.

FORMATION 1. SOIL

Animals that live in soil are dependent on various factors for existence. Clay, humus, sand, or rock each has its characteristic animals which are influenced more or less by temperature, moisture, aeration, soil reactions, and the presence or absence of particular chemical substances and organisms.

Insolation is apparently more important than air temperatures in warming soil, and its effectiveness decreases with altitude (Shreve 1924). Maximum soil temperatures are generally more variable than minimum. The spring and autumn "overturns" in temperature are very important for soil animals. McCulloch and Hayes (1923) found that the white grub came nearer the surface after the spring overturn and descended after that in the autumn. The ranges of temperature variations decrease with increases in depth. McCulloch and Hayes give the following average annual ranges for the soil in Kansas: at a depth of 1 ft., 28°C.; 3 ft., 21.4°C.; 6 ft., 15.7°C. They say: "The soil responds to great outside temperature changes slowly. The temperature at 1 foot responds the same day, at 2 feet about one day later." At the beginning of March the lowest temperature was found at a depth of about 1 ft.; during warm periods in winter the temperatures were about the same at all depths up to 6 ft.; in summer the surface had a higher temperature than greater depths; in winter the opposite was true. When soil was covered with snow, temperatures at a depth of 6 ft. did not go below 4.2°C., though air temperatures above reached −25.0°C. (Mail 1932). Many soil insects burrow deeper when surface temperatures become unfavorable (Hallock 1935). Soil insects are

generally able to endure wide variations in temperature, and the same is known to be true of earthworms, isopods, and many other subterranean animals (Cameron 1913). Koch (1915) states that soil protozoans develop best between temperatures of 8–30°C. Some animals are able to endure cold periods because they associate themselves with decaying organic matter which keeps them from freezing. Bumblebees that live underground cool their nests by fanning with their wings and keep their nests warm in cold weather by body heat and insulation with wax and other materials (Himmer 1933). Temperatures may affect soil animals through their influence on moisture. Cold air can hold less water vapor than warm. Earthworms most often make excursions over the surface of the ground when humidity is high and temperature is low (Heimburger 1924).

Water in Soil.—The amount and the form of water in soil are important factors for soil animals. Shade and protection from the action of wind generally permit greater numbers to exist. Soil insects may be drowned by an excess of gravitational water. On the other hand, soil Protozoa are usually encysted except for short periods after rains. Certain tiger-beetle larvae plug their burrows with pellets of clay when the soil is dry (Shelford 1912). Ants usually excavate most actively just after rains. Wet soil is often poorly aerated. Porous soils are usually best for larval insects because they contain plenty of oxygen, but some soil-inhabiting fly larvae can survive for long periods without oxygen (Cameron 1913). Collembolans are influenced by soil temperatures and moisture changes, which in turn are regulated by soil cover (Davidson 1933, 1934).

Soil Reaction.—The reaction of soil often limits the distribution of subterranean animals. Wherry (1922) has found that the greatest number of plants, both species and individuals, usually grow in soil that is slightly acid. Minerals like lime may serve two functions, furnishing material that is necessary for metabolism and making soil reactions alkaline. Coville (1914) found that more fungi and animals that promote decay (bacteria, earthworms, etc.) were to be found in an alkaline soil. Waksman (1924), however, has shown that fungi increase with fertilizers that tend to increase soil acidity. A dogma has long been current that earthworms cannot live in soils that have an acid reaction. For example, Arrhenius (1921) states that earth-

worms were found only in soils where the pH values ranged between 6 and 7, which is barely on the acid side of neutrality. Phillips (1923) states that, though earthworms are scarce in markedly acid soil, he has observed one species living where there was acidity represented by pH 5, and Wherry (1924) has noted a species, *Helodrilus lonnebergi* Michaelson, that lived in peat where the pH was 4.7–5.1. Various species of protozoans are also known to have a wide range of toleration in relation to soil reactions.

Characteristic Soil Animals.—Characteristic inhabitants of the soil are various Protozoa, earthworms, tardigrades, insects (especially in larval stages), millipedes, isopods, termites, ants, amphibians, reptiles, rodents, and moles. Many other animals may invade the soil temporarily, digging burrows of their own or inhabiting those made by other species. Where conditions are favorable, enormous numbers of soil animals may be present. Earthworms have been estimated at hundreds of thousands per acre (Darwin 1881, Thomson 1911, Branner 1914). There may be thousands of millions of nematodes (Cobb 1914), and each species is adjusted to certain depths, reactions, temperature and moisture ranges, etc. (Brown 1929, Thorne 1930). Protozoa may range from 30,000–150,000 per cubic centimeter, and bacteria from 220,000–2,460,000 (France 1911, Waksman 1932). McColloch and Hayes (1922) have given an excellent review of the literature relating to the number of soil insects that may occur and report such numbers as 3,586,088 per acre, 84–300 per square foot, etc.

> There is no doubt that in areas where ants or termites occur the number of individuals present is enormous. It might also be said that soils rich in organic matter usually contain thousands of Thysanura, Collembola, and immature stages of Diptera. . . . Insects may be said to utilize the soil for shelter, protection, materials for abode, food, moisture, air, heat, and as an avenue for travel.

In Minnesota, Mohr (1936) found four to six pocket gophers per acre, or 938.4 to 1,252 g., live weight. Ground squirrels are at times even more abundant in favorable places (Edge 1934, 1935). In moist soils in Michigan shrews dig burrows and store snails in them for food (Shull 1907). Bornebusch (1930) and Tradgardh (1933) have made extensive studies of the numbers of animals in the soils of northern Europe.

Depth of Animals in Soil.—Usually, soil animals are quite close to the surface. Cameron (1913) found few insects below a depth of 3 in. but noted that larvae usually burrowed deeper before pupating. In the Belgian Congo, Steel (1913) found the burrows of termites 5 ft. below the surface. The pocket gopher seldom goes below a depth of 2 ft. Darwin (1881) observed that earthworms descended to a depth of about 6 ft., and burrows somewhat deeper than this have since been reported. Earthworms may be arranged more or less in strata, some species regularly being found at greater depths than others (Bretschler 1901, Shindo 1929). The burrows of the prairie ant may be 9 ft. deep (Hungerford and Williams 1912). Those of the prairie dog sometimes extend to a depth of 14 ft.

Adaptations of Subterranean Animals.—Burrowing animals are, in general, cylindrical in form, stocky, and robust. McCulloch and Hayes (1922) say in regard to insects:

> Certain general modifications might be mentioned as associated with subterranean life. Usually the body is more elongate, the sense organs more highly developed, the eyes and wings reduced or wanting, and metamorphosis simple. While all these modifications do not apply to all soil insects, it may be stated that they are often present in direct proportion to the amount of time the insect lives in the soil.

Subterranean representatives of groups that have limbs in other habitats are often apodal (amphisbaenians, caecilians, etc.). Other burrowing animals (mole, cicada nymph, etc.) have enormous digging limbs developed near the anterior end. Some small animals burrow by packing the dirt toward the sides of their burrows. The earthworm progresses by eating soil as it burrows. Hancock (1911) described a burrowing spider which makes its tunnels by repeatedly spinning a disk which adheres to the sand and is then removed. Soule (1900) observed three species of burrowing caterpillars which did not spin but packed the soil firmly to form a cocoon before they pupated. The digger wasps excavate with their legs or mandibles and may use clay or leaves to make their nest cells strong. Ants often place stones or leaves above their nests to protect them from wind and rain. Burrowing rodents that dig largely with the front feet may have small hind limbs, and the pelvic girdle is often more or less modified so as to permit them to turn about in their burrows

and at the same time be able to bear young. Burrowing mammals with narrow pelves (mole) commonly push the dirt to either side and crowd their way through the soil; those with broad pelves (pocket gopher) throw loose dirt back with the hind legs and at intervals push it up to the surface (Chapman 1919, Grinnell 1926). Many burrowers use special means to keep the soil from caving into their burrows. The earthworm lines its galleries with slime; spiders and insect larvae often spin a lining for their burrows; some tiger-beetle larvae cement sand grains together with saliva. The eye of the hedgehog is retracted into the skull underground but protrudes when the animal is above the surface; that of the mole is degenerate. Baumgartner (1905) has pointed out that mole crickets are unusual among orthopterous insects because both sexes stridulate. He believes that the notes of these insects serve both for giving notice that a burrow is occupied and for finding mates. He also calls attention to the fact that the soft abdomen of the mole cricket permits the animal to turn readily in its burrow; it is protected from attack by repugnatorial glands. The loss or degenerate condition of visual organs in certain burrowing animals is often compensated for by the greater acuity of chemical or tactile senses.

Food of Animals in Soil.—Subterranean animals are directly or indirectly dependent on vegetation for food. Some feed largely on the underground parts of plants (white grub) or draw plants into their burrows without emerging (pocket gopher); others come out on the surface and drag down leaves, fruits, and other parts of plants (earthworm, ground squirrel); some raise fungi in underground gardens (ants, termites); some depend largely on decaying organic matter; and others are predaceous, seeking food above or below the surface (centipedes, many species of nematodes). Earthworms often allow leaves to decay underground and perhaps depend for food as much on the fungi that develop as on the leaves. Digger wasps are specialists in hunting different kinds of animals, and each knows the habits of its prey. Hartman (1915) states that these insects fall into two groups: (1) those which feed their larvae daily and (2) those which sting their prey and store it away in nests. The first group are believed to be more primitive. Soil insects fall into four groups, according to Butovitsch (1933), in regard to food habits: (1) feeders on humus and decomposing plant materials, (2) feeders on the roots

of grasses and herbs, (3) feeders on the roots of trees, and (4) predators. The common mole requires a variety of food, not only devouring insects and earthworms but also continually consuming some vegetation. One mole ate an amount equal to 66.6 per cent of its body weight in 18 hours (Hisaw 1923). Certain predators are specially adapted to prey on burrowing animals. In prairie-dog towns burrowing owls and rattlesnakes devour the young rodents. Bull snakes (Fig. 100) are persistent enemies of pocket gophers and ground squirrels (Hisaw & Gloyd 1926). They pursue such animals into their burrows.



FIG. 100.—Bull snake killing a pocket gopher by constriction. (*From Hisaw & Gloyd* 1926.)

Difficulties of Life in Soil.—Though animals that live in soil are protected from most dangers, they are particularly subject to others. The white grub escapes from desiccation, rapid changes in temperature, and predaceous enemies that work aboveground but is subject to attacks by a fungus and is devoured by moles. Many subterranean animals cannot endure desiccation, and many (largely those that come to the surface for food) cannot endure water in unusual amounts. Rains make extra work for ants by filling up their galleries. Ants more commonly burrow in clay than in sand, which caves in easily. Many ants, wasps, bees, spiders, and rodents build towers or mounds which keep water from flowing into their burrows. Prairie dogs are probably sensitive to barometric changes, for they begin to bank up dirt

about their holes several hours before rains, often even when it is not cloudy. Prairie dogs build vertical tunnels toward, but not actually reaching, the surface at the intersections of their anastomosing burrows. When their "towns" are inundated, they are able to live for several hours in the air in the vertical blind passages (Foster 1924). Some burrowing animals use their burrows only as refuges from enemies. The guano birds along the coast of Peru escape the condors and buzzards by their subterranean life and nocturnal flights for food (Coker 1919). Harvester ants and prairie dogs cut down the vegetation near the entrances to their burrows, so that the view is unobstructed.

Character of Soil and Animal Life.—The character and the condition of the soil are usually important factors for burrowing animals. Gleason (1909) found that there was little or no animal life in loose soil that overlay rock unless it had a depth of at least 5 cm. Shelford (1911) showed that several species of tiger beetles, though their larvae were much alike in structure, chose different types of soils for depositing their eggs. Cameron (1913) observed certain wasps that burrowed in sandy soil where the sun shone part of each day, the soil being loose and easy to excavate on the surface but moist enough not to cave in easily below. Turner (1922) described a wasp that made burrows near water and strengthened the walls of its nest by plastering them with moistened clay. Insect larvae usually avoid clay soils, but a few frequent them, probably because their firmness compensates for their tendency to hold moisture and maintain a rather low temperature. Gray sand is more stable and contains more organic matter than white, which is easily blown about (Warming 1909). Humus usually supports an abundance of plant and animal life. Most species of earthworms live in soils where reactions range from pH 7.0–7.8 but may occur in those between pH 5.4 and 8.3 (Allee, Towik, Lahr, & Hollister 1930). Burrowers usually excavate most actively when the soil is in the best condition for digging. For example, pocket gophers usually work most in the spring. Good soil for plowing is good soil for the extension of old burrows and the beginning of new excavations. Some animals are little affected by the nature of the materials in which they burrow. Certain Australian termites burrow through stone and sheet lead (Stead 1900); dermestid larvae make burrows in salt (Blanford 1899).

Holdhaus (1910) classifies all animals that live in soils as terricolfauna and separates them into four groups: (1) stone-indifferent animals, which are widely distributed, (2) petrophile, associated with stones; (3) psammophile, in sand; and (4) halophile, a somewhat doubtful group limited by salts. After fires soil is harder, less porous, and supports fewer animals (Heyward & Tissot 1936).

Association *a*. Clay Soils

Many of the animals that frequent clay soils depend on the surface (Fasciation 1) for food (tiger-beetle larvae, isopods, prairie dogs), and in a dry climate many are able to go without water except that which occurs in their natural foods. When humus is mixed with clay, earthworms and other animals that live more or less permanently below the surface (Fasciation 2) are also present. Insect larvae like white grubs are usually found in humus soils but may live in clay if roots and other materials are present for food. Prairie dogs apparently prefer clay soils because they do not cave in readily.

Association *b*. Humus Soils

Humus usually supports vegetation and many animals, but the types of plants and the number of animals present may be limited by such factors as the presence of excessive amounts of acids or alkalies, northern exposure, and high altitude, so that the temperature is continually low. The animals that depend on the surface (Fasciation 1) and those that live more or less permanently underground (Fasciation 2) are usually well represented.

Association *c*. Sandy Soils

Sandy soil is easily moved, and hence burrowing in it is easy, but it caves in readily and does not hold water well. It usually contains few burrowing animals that live more or less permanently underground. Many of the animals that live in sand make burrows beneath plants, where the roots prevent caving.

Association *d*. Rocks

Animals that frequent holes and cracks in rocks are largely species that may live in similar situations in other habitats. Woodchucks often dwell in rock "slides" but may also dig holes

in fields. Ants, spiders, and snails that live in crevices may maintain colonies in the earth, in wood, or in rock. Though animals occasionally burrow in rock, there is no established fasciation below the surface. There is a bee in Colorado that regularly digs holes in sandstone and collects food only from cactus blossoms (Custer 1928).

FORMATION 2. CAVES

In caves there is usually very little annual variation in temperature and humidity. In the deeper parts of Mayfield's Cave, Banta (1907) found that there was less than 2°C. variation throughout the year. Light is present only near the mouth, and animals that live permanently in caves usually exist in total darkness. Food all comes from outside, directly or indirectly, and organic remains are of great importance. Racovitza (1907) says that inanition is the usual state of cave animals. Large animals (including man) leave excreta and bring in objects that are eaten. Streams wash in Protozoa, annelids, crustaceans, insects, algae, seeds, wood, and other things that may serve as food. Fungi are an important source of nourishment for thysanurans and probably for other animals also.

Adjustment of Animals to Caves.—Banta (1907) states that cave animals are usually most abundant where there are (1) considerable moisture, (2) organic remains, and (3) loose stones or other materials that furnish small crevices for hiding. Some animals show a gradation in their distribution according to their nearness to sources of light; others do not. Most speleologists agree that caves have been populated by animals from surrounding epigean regions. Cave animals are fitted more or less for cave conditions before entering, but some have become further adapted and at present are strikingly adjusted to a stygian existence. Sometimes habits of periodic activity persist among animals that live in the innermost recesses of caves, though the changes that usually accompany day and night do not occur. In general, there are not fixed and limited periods of reproduction at particular seasons. Hibernation and estivation on account of seasonal variations in temperature and moisture are rare phenomena among permanent residents. The uniformity of humidity and temperature conditions are correlated with the fact that many cave animals are stenothermic and stenohydric. Raco-

vitza (1907) says that the high humidity is favorable to many species because there is little danger of desiccation. In this connection he cites snails that do not form epiphragms to close their shells. Among cave animals organs for receiving tactile stimuli are often large; eyes and pigment are commonly degenerate.

Association *a*. Transient Cave Animals

Trogloxènes and Troglophiles.—Animals may enter caves by accident and remain for a time, and others habitually use caves as retreats. Racovitza (1907) classified cave animals in three groups: (1) trogloxènes, which are facultative inhabitants of caves and have some adaptations that fit them for cave life; (2) troglophiles, which live more or less continually underground but have relations with the epigean world; and (3) troglobies, which are wholly troglodyte. Such animals as raccoons, chipmunks, woodchucks, mice, foxes, weasels, bears, salamanders, frogs, beetles, crickets, spiders, phalangids, mites, myriapods, pseudoscorpions, isopods, and snails (Fasciation 1) wander into caves and remain for a longer or shorter time. Some spend the night; others go in and out for months or years; others use the caves for hibernation or estivation. Flying animals (Fasciation 2) often make use of caves. Hahn (1908) states that certain bats spend five-sixths of their lives in caves where temperature varies little and light is absent. They come to the mouth of the cave at irregular intervals but do not go outside when it is cold or when the sun is shining brightly. Each bat does not roost continually at a particular spot, but favorable situations are usually occupied. Mosquitoes, moths, flies, and other insects hibernate in caves (Banta 1907).

Association *b*. Permanent Residents in Caves

Troglobites.—Many air-breathing animals live permanently in caves, but they usually constitute only a small part of the population. In 27 Yucatan caves the writer (1938) collected 306 species of animals. Of these about 10 per cent were troglobite; 25, troglophile; and 65, trogloxène. Troglobites included collembolans, crickets, ants, millipedes, chelonethids, spiders, and fishes. In the United States there are characteristic blind beetles and salamanders. In eight Hungarian caves Kolosvary

(1934) found among 20 species of spiders: eutroglobionts, 0; troglophiles, 10; trogloxènes, 10. McIndoo (1910) has described the adaptations and habits of two cave spiders—a linyphid and an epeirid. One of these is found only in total darkness, where considerable moisture and places for snares are present, but the other may occur near the mouth of a cave where there is some light. These spiders build webs and catch flies, thysanurans, and myriapods. They also eat each other. The web of one species is so fine that it will shed water. The eyes and eye pigments of cave spiders show various degrees of degeneracy. The epeirid studied by McIndoo was sensitive to light, but the linyphid was not. The fact that many cave animals show more or less degeneracy in visual organs has been mentioned. Eigenmann (1909) and his students have studied the eyes of cave vertebrates and find various degrees of loss of eye structures and functions. Banta (1910) showed that an aquatic cave isopod (Caecidotea) did not respond to light that had an intensity below 60 candle meters, but an epigean isopod (Asellus) responded to 1 cm. Banta and McAtee (1906) studied the light reactions of a cave salamander, *Spelerpes maculicaudatus*, and found that larvae were much more responsive than adults. This species deposited its eggs in January, and the young were seen only in the deepest parts of caves, but the adults were sometimes found under logs a mile from any cave.

PROVINCE B. ON SURFACE OF THE SOIL

Animals that live above the surface of the soil are exposed to light, temperature variations, and winds. They are more readily caught by enemies than animals that live underground and are in more or less danger of being frozen, overheated, or dried up.

FORMATION 1. SURFACE

Surface Organisms.—The animals and plants that are found on the surface of the earth are not all properly to be classified there. At times, certain burrowing animals may come from below, and animals that commonly live in strata above may visit the earth's surface through intent or accident. There are animals, however, that have their primary habitat on the earth's surface. Many of these are nocturnal or diurnal and may,

during inactive periods, become part of the thigmotactic fauna which hides under stones, logs, and loose bark and in other crevices. Animals that stow themselves away in sheltered nooks are protected from desiccation and extreme temperatures. Many surface animals have great resistance to low or high temperatures. Moore (1899) observed that the enchytraeid worms that lived on Malaspina Glacier burrowed into the snow when the direct rays of the sun struck them and were active chiefly at night. He also kept a Limnodrilus in a glass of water on his windowsill, where it alternately froze and thawed all winter but remained alive. On the glacier the temperature during the day reached 13°C. and at night was about 0°C., yet the surface was populated by gulls, moths, spiders, flies, thysanurans, and worms. It is said that the agricultural ant of Texas may work until the temperature of the air reaches 65°C., and that of the soil 45°C. When conditions are favorable, many surface animals may occupy an area. Their colors may match with great accuracy the backgrounds on which they usually rest, but there are many exceptions, particularly among nocturnal animals, which are often black. Cameron (1917) counted the numbers of insects occurring on soil and low vegetation in summer. On plots 1 ft. square he found in a meadow 4–32 and in a pasture 3–122.

Periods of Activity of Surface Animals.—Many factors that exert influences upon the animals are intermittently associated with the surface of the soil. Many protozoans usually encysted in soil swim about at the surface for a time after rains (Goodey 1911). Henderson (1905) affirms that land snails become active when the barometer falls, often as much as 6 or 8 hours before rains. Most species are not active during rains, and Henderson therefore concluded that moisture in the air was more potent than that on the ground. Glacier worms are active when there is little or no light (Moore 1899). Pieron (1908) says that snails and actinians may migrate out of the ocean at night, supposedly because the algae cease to carry on photosynthesis and there is insufficient oxygen for their needs.

Influence of Soil Variations on Surface Animals.—The most important factors in determining the character of the habitats on soil surfaces are variations in water and soil constituents. Rock and, to a lesser extent, sand are often dry and subject to rapid

changes in temperature. Humus is less variable and usually supports more vegetation, hence affording more shelter from sun and wind. Wet soils, though they help surface animals to resist desiccation, are often sour (or acid) and consequently, as a rule, furnish little living organic food.

Association *a*. Surface of Wet Ground

There are many animals, like certain earthworms and salamanders, that require considerable water and are, therefore, confined to moist situations. There are also animals, like certain ants, that may live both in more or less dry and in moist situations.

Fasciation 1. Burrowing Animals.—Burrowing animals may be absent from wet ground on account of excessive amounts of water or of dissolved substances (usually salts or acids), but in many localities earthworms, shrews, crayfishes, crabs, and other subterranean animals come from their retreats, especially at night, and forage over the surface. Some ants that live on wet soils raise their nests above the surface as mounds, but in drier soils the galleries of the same species may be largely subterranean. The depth to which the galleries of such ants extend varies with the distance of the water table below the surface. Mound builders, *Formica ulkei* Emery, in the northern United States descend to water and spend the winter in great groups just above it (Holmquist 1928). Another northern ant, *Prenolepis imparis* Say, is active in Massachusetts at intervals throughout the winter (Wheeler 1930). Termites often frequent wet ground, and thus escape from their chief enemies, the ants (Branner 1912).

Fasciation 2. Surface Animals.—On wet soil snails, amphibians (frogs, toads, salamanders), centipedes, millipedes, isopods, grasshoppers, spiders, and snakes are characteristic. Many of these animals hide in crevices at times.

Fasciation 3. Animals from above Surface.—Species that normally live above surface habitats may temporarily become part of the surface population. During the day, wasps, birds, and other animals seek food or a resting place; at night, such animals as skunks, raccoons, and mice are foraging.

Semiaquatic Animals.—Certain animals that live on wet ground are in a state of transition from aquatic to land habitats. Crabs and crayfishes live in burrows, which they usually leave

only at night. Crab holes are breeding places for certain mosquitoes, and other small animals live in them. In Missouri, Creaser (1931) found more than 6,000 animals in a quart of water taken from a crayfish burrow. These consisted of three species of crustaceans: an ostracod, a copepod, and an amphipod. Bishop (1920) describes a salamander that lays its eggs in sphagnum moss. The eggs require moisture but cannot live in moss that is saturated with water.

Association *b*. Surface of Medium-dry Ground

As soil becomes drier it is less favorable for some types of burrowers (Fasciation 1) which form part of the surface association at times, and is more favorable for others. Earthworms gradually give place to insects and their larvae, rodents, tortoises, etc. Soil that contains an intermediate degree of moisture is usually humus and often supports an abundance of earthworms, grubs, ground squirrels, moles, and other burrowers. On the surface of the soil (Fasciation 2) are characteristic beetles, ants, grasshoppers, crickets, myriapods, spiders, slugs, voles, rabbits, etc. Perhaps tent-weaving spiders and ants are as characteristic as any animals in such situations. In undisturbed areas in Mississippi Haug (1934) found one colony of an ant, *Iridomyrmex humilis*, on every 125 sq. ft. of ground surface. In any locality there is often a marked difference between the animals that live on exposed soil and those that are found beneath the shade of vegetation. Usually there are fewer surface animals in the latter habitat, probably because many climb upon the plants. Shelford (1912) found that the surface animals among cottonwood trees were largely swift, predaceous, diurnal, and wary. On cloudy days most of them hid underground or in crevices. Mesophytic vegetation harbors many animals (Fasciation 3) which at times take part in the activities on the soil surface. Some fall off the vegetation and move about; insect larvae descend to the ground to pupate; squirrels come down to bury nuts; etc.

Association *c*. Surface of Dry Sand

Sand is loose and readily moved by winds unless it is wet or is held together by plants. Animals that live on it can easily cover themselves to escape extremes of temperature or to avoid drying out, but many of them are able to endure considerable desiccation.

Wasps, spiders, mice, and other animals dig burrows (Fasciation 1) and at times run over the surface of the soil with spiders, insects (grasshoppers, crickets, beetles, etc.), snakes, lizards, sand grouse, plovers, antelopes, and rodents that do not make excavations (Fasciation 2). Buzzards, dragonflies, and other predaceous animals (Fasciation 3) often hunt over sandy areas, where the scantiness of vegetation makes it easy to observe small animals that may serve as food.

Sand Dunes.—Shifting bodies of sand are moved about by winds in many localities. Such changing surfaces (Fig. 101)



FIG. 101.—A young sand dune with reeds and shrubs holding the sand. (*From Weaver & Clements* 1926, *after Fuller*.)

are populated by characteristic plants and animals. Grasses and vines often have underground rootstalks; shrubs and trees are often xeric in character, but in later stages of succession mesophytic types may become established. There are characteristic insects, reptiles, birds, and mammals that live on sand dunes. Some of these (Bembex) are nocturnal or crepuscular and have little ability to endure desiccation or extreme temperatures; others (Melanoplus) have wide ranges of toleration. The digger wasp, *Bembex pruinosa*, Fox, while making its burrows avoids becoming overheated by ascending at frequent intervals to cooler strata in the air above. Mutillids which parasitize

the larvae of bembicids are wingless and cannot leave the surface of the sand. They are able to endure high temperatures (Chapman 1931). Burrowing spiders avoid heat by descending to the bottoms of their web-lined holes.

Association *d*. Surface of Rocks

Exposed rock surfaces are dry because they cannot retain much water and are subject to great daily changes in temperature, for they become very hot when the sun shines and cool rapidly when it does not. Rock rarely contains a burrowing fauna; but when it is broken into pebbles or contains caves, the number of animals that it may support is greatly increased. The vegetation cover of rocks is usually scanty and consists largely of lichens and mosses. Notwithstanding the severity of conditions of life on rock surfaces, there is usually a scanty animal population. Snails, ants, spiders, and rodents live in crevices (Fasciation 1) and come out at favorable times to feed. Rabbits and other animals that frequent the surface of the ground often rest in rocky situations, where the lack of vegetation leaves an unobstructed view and thus prevents the unheralded approach of predaceous enemies. The open spaces also bring foraging animals like owls, swallows, robberflies, and dragonflies and those that come to play about or mate, like butterflies and midges (Fasciation 3). Many of the animals found on rocks are transients from other habitats.

Cliffs.—Where rock surfaces slope so abruptly as to form cliffs, they are often frequented by sea birds, swallows, eagles, hawks, wasps, and other animals which thus secure safe nesting sites and seek food elsewhere. They may also be used for the observation of the lowlands by predaceous animals such as eagles. ✓

FORMATION 2. TERRESTRIAL PLANTS AND ANIMALS

Every naturalist knows that land animals are arranged in associations that are primarily related to plants. The number of individuals and the character of species are usually natural results of what different types of plant associations are able to furnish in the way of food, shelter from enemies and the drying action of air, protection from temperature changes, and other desiderata.

The terms forest, grassland, and desert are a subconscious classification of the principal climatic formations and are only another way of expressing the water content of soils (Waller 1918).

On the sand dunes near Chicago, Sanders and Shelford (1922) found species of animals distributed as follows: surface, 10; herbs, 34; shrubs, 38; trees, 11. Such numerical differences between the animals in habitats as represented by various types of vegetation are more or less typical of all localities where animals live on land.

Association *a*. Forests

Types and Characteristics of Forests.—Compared to open-ground habitats like prairies, forests are more stable. Their humidity and temperature vary less and more slowly. Barrell (1917) believed that the dangers of life are less in trees than on plains and stressed this fact in connection with the characteristic animals in the two formations. There are three principal types of forests: (1) coniferous, (2) deciduous dicotyledonous, (3) evergreen dicotyledonous. In their "Plant Ecology" Weaver and Clements (1938) classify types of forests in North America as Subalpine, Lake, Coast, Montane, Deciduous, etc. Under deciduous forests they include Maple-Beech, Oak-Chestnut, and Oak-Hickory. Such climax groups are composed of different dominant species of trees which have developed in various regions. Forests usually progress to their climax more rapidly on clay soils than on sand, and in temperate and tropical regions conifers may persist in sandy regions because they have less available water. Animals that live in forests made up of pine trees are, on the whole, more exposed to light and variations in temperature and humidity than those that live in broad-leaved forests. Animals that live in forests have the food resources that result from photosynthesis and also have a certain degree of shelter. The trees stand above the ground and on account of this fact and also through their absorptive, transpiratory, and other activities related to water maintain a certain humidity balance in the atmosphere, which is thus usually prevented from becoming extremely wet or dry. For similar reasons the temperature remains more uniform. Large forested areas transpire moisture continually and thus add water

to the atmosphere. This is carried by prevailing winds and may profoundly influence even the climates of nonforested areas to the leeward (Zon 1913). In open spaces twice the amount of water evaporates from porous cups as beneath forest cover; trees shade soil and litter so that temperatures never reach such high extremes as in the open (Stickel 1933). Shelter is furnished by trees in another sense: their broken contours furnish many safe resting and hiding places for animals. As litter from trees accumulates on the ground, insulation and shelter are present there also. Logs and fallen leaves furnish refuges for amphibians, insects, mammals, etc. Some animals use forests as hiding places and find food elsewhere. Deer crouch in the shade of forests but often feed upon the grass on open ground. A lizard in New Zealand spends most of its active life in water but climbs up 12–20 ft. into trees to bask and sleep (Symonds 1912). Dense forests are unfavorable for many animals because there are little light and food near the ground; most of the inhabitants are arboreal and live in or near the treetops. Bates and Zon (1922) in their discussion of research methods in forestry take up many matters of general interest and give tables that relate to the determination of the state of various factors, such as barometric and osmotic pressures, freezing points, alkalinities, and salinities. Matoon (1936) has published lists of forest trees and forest regions in the United States, with illustrations of various types. These include such remote regions as Puerto Rico and Hawaii.

Adaptations of Forest Animals.—Animals that live more or less permanently in or among trees show various adaptations to forest life. Hesse (1921) asserts that animals in forests have a tendency to be large, strong, and muscular compared to those in the open country. For an arboreal animal speed is on the whole less desirable than ability to cling firmly and to hide from other animals. Arboreal animals are generally good climbers, and such specialized structures as the feet of monkeys, squirrels, sloths, and tree frogs are admirably suited for locomotion among branches. Many have balancing organs which keep them from falling from smooth branches (tails of squirrels, monkeys, and certain birds). Some forest animals (tree frog) are excellent jumpers and commonly leap to seize their prey or to escape from enemies. Many arboreal animals are able to sail or fly. Morse (1904) found that

the wings of forest orthopterans were unusually long, and he believed that this was to facilitate passages across open spaces. A number of typical forest animals sail or fly (flying foxes, flying squirrels, bats, Draco, and the Javan tree frog). Clark (1925) has contrasted the animals of the South American and Malayan forests. In the continuous leafy canopy of the former, prehensile tails are a great advantage. Fireflies also find ideal conditions. In the more open forests of the east, gliding is more advantageous, and gliders are correspondingly common. Some caterpillars that feed on the leaves of forest trees spin threads and descend on them to the ground for pupation. Rodents with their gnawing teeth, and woodpeckers with their peculiar beaks, are specially equipped to make and inhabit holes in trees. They are protected from many enemies by the small size of the entrances into their dwellings. The holes made by such animals are often inhabited by others. Many small boring animals are absolutely dependent on the wood in forests for food and shelter. Hingston (1920) calls attention to the way in which the abdomens of certain ants that climb up and down tree trunks are attached. In the case he cites, the abdomen stands at right angles to the thorax, which is the position that it would tend to assume on account of its weight and slender pedicel when an ant was moving downward and is thus no greater impediment when the ant moves upward. Both Hingston (1920) and MacGregor (1920) have noted that forest birds are commonly gregarious. The former believes that insectivorous species are thus able to capture prey more easily because there are more beaters to raise the insects and more watchful predators to prevent escape. MacGregor believes that birds of different species often consort together in order to keep a better watch against enemies. The colors of forest animals often resemble with great accuracy the backgrounds against which they are seen. There are simulators of bark, light and shade shining through foliage, leaves, twigs, etc. The chameleon and the tree frog are examples of arboreal animals that possess remarkable ability to change their colors. Collins (1922) has given a very interesting account of certain adaptations of primates to arboreal life. The eyes of men and monkeys differ from other mammals in having a small lens and cornea which are associated with the presence of a highly centralized retinular area of sharp vision. They are unique among mammals in having parallel optic axes.

The recession of the snout in primates has been associated with (1) the substitution of the hand for it as the chief tactile organ, (2) the decrease in the use of the jaws for tearing and seizing, and (3) the decreased importance of the sense of smell. In the tree-tops there is little value in being able to follow odor trails, but it is of great importance to be able to see clearly, particularly in judging distances. After studying fossil insects from amber and comparing them with insects caught in pitch exudations in modern forests Brues (1933) concludes that since Tertiary times primitive forest insects have decreased and modern types have increased.

Food in Forests.—There is no dearth of food in a forest. Many animals that depend directly on its plants are specialists and require particular species or parts. For example, many species of insects attack the basswood. In the foliage there are 4 bugs, 6 beetles, 52 lepidopters, and 1 gallfly; on the bark, 7 scale insects; 15 beetles and 1 lepidopter bore about in the wood (Gibson 1904). In his report on insects associated with trees Felt (1905–1906) states that bark borers, twig borers, ambrosia beetles, and leaf feeders are characteristic among pines; borers, fungous beetles, injurious and beneficial leaf frequenters (phytophagous and predaceous), and gall insects are typical among deciduous trees. The important insects feeding upon trees are said to be sawflies, cynipids, cecidiomyids, boring beetles, chrysomelids, curculionids, scotylids, lepidopters, aphids, and scales. Weiss and West (1922) found that insects in moist woods usually injured the vegetation very little. Some fed on foliage, but others ate rotton wood, fungi, or other substances. These investigators give the following percentages of insects having various food habits: phytophagous, 37; saprophagous, 35; predaceous, 20; parasitic, 5. In a thicket the percentages were: phytophagous, 63; saprophagous, 9; predaceous, 19. The same writers later (1924) found that there were more species of saprophagous insects in woods and more flower and pollenizing insects in open fields. It goes without saying that in forests as in other habitats there are fewer predaceous than phytophagous animals.

Reproduction of Forest Animals.—The reproductive habits of many forest animals are adapted to life in trees. Some tree frogs carry their eggs on their backs; others deposit them in the

water contained in epiphytes; others roll their eggs up in leaves, and the hatching tadpoles fall into water below; the Javan tree frog incloses its eggs in nests within rolled leaves which contain water, and the tadpoles complete their metamorphosis in the tree-tops. Many animals build nests or utilize holes in trees for breeding purposes. Galls furnish food and shelter to the larvae of various insects. Girdlers deposit eggs in girdled twigs; the larvae live on the dying wood for a time, and the twig may fall off and carry its guests to the ground.

Borers in Wood.—The many insects and the few other animals that live in wood constitute an interesting part of the forest population. These animals have means for boring and are usually limited in their ranges of food, temperature, and moisture toleration. Graham (1922) has classified into five groups the insects that live in logs: (1) those that require fresh cambium for food and usually have a brief metamorphosis; (2) those that require fresh cambium for their early development but later are able to feed on outer sapwood; (3) those that feed first on cambium, later on sap- and heartwood; (4) those that pass their entire period of metamorphosis in heartwood; and (5) those that do not depend on wood directly but feed on other organisms that live in it. Graham found that the subcortical temperature of logs exposed to the sun might reach as high as 60°C. and that 48°C. was fatal to all boring insects. The bark of some species of trees furnishes efficient thermal insulation, however, and temperatures inside it never reach 48°C. Insects to some extent were found to be assorted in logs according to their degree of exposure to the action of the sun. The food value of a tree is, of course, determined largely by its chemical composition, but its availability may be markedly influenced by its temperature and water content. A Xylographus beetle feeds on ambrosia fungi in wood (Hopkins 1898). In this case the females winter over in old brood chambers and in spring go to sick or dead trees and cooperate in making a home. One female excavates while another shoves out the chips. A tunnel is thus made, and each female constructs side galleries into the heartwood where she deposits her eggs. The entrance to the tunnel is closed and thus enemies are excluded. Many of the large animals, such as rodents and woodpeckers, that live in trees usually work largely in deadwood that has been softened

by decay. Succession in logs has been studied by Adams (1915) and Savely (1939). The latter points out that fungi play a leading role in transforming logs from habitats suitable for phloem feeders to those which may be used by wood feeders.

Forest Litter.—Fallen leaves, branches, and trees form a continuous carpet over the soil in a forested area and constitute the upper layers of soil as recognized by pedologists (Fig. 16). This cover conserves moisture and equalizes temperatures. Leaves and other debris make a rough cover over the surface. Just above the sub-soil, fungi and plant roots bind organic remains into a continuous felty layer. This humus layer has been differentiated into two types: (1) mull, when it is formed from broad leaves; and (2) mor, when from needles of conifers (Romell 1933). There are more fungi in the latter, and more bacteria in the former. Careful counts of animals that live in litter and the upper layers of soil have been made (Bornebusch 1930, Jacot 1935, 1937, Tragardh 1933). Thousands of animals live in forest litter. Among these nematodes, earthworms, millipedes, centipedes, mites, spiders, insects, and snails are common. Jacot (1935) has given a very entertaining account of the animals in a square foot of forest litter:

> In the case of the forest carpet there is one millipede, proturan, thrip or plant-eating insect larva for every thirty springtails or every fifty vegetarian mites. In the case of the predators there is one centipede, ant, spider, pseudoscorpion, beetle or predaceous bug for every ten predaceous mites. Thus one can say that mites and springtails are numerically the dominant groups. Whereas all other groups are numbered by units or tens, these two are numbered by hundreds (predaceous) and thousands (vegetarian). Among the springtails, there is always one or a few species in great abundance, while the other species are numbered by units and tens. The same is true among the mites.

Many litter animals are adapted to special and peculiar conditions. For example, a freshly fallen spruce needle is first attacked by fungi; then a mite lays eggs within it, and the whole next generation is passed in the needle, until mature individuals leave to find mates (Jacot 1936).

Consociation *a*(1). Coniferous Forests

Conifers are xerophytic, in that they are adapted to a low rate of transpiration, but they need an abundance of light.

Coniferous forests occur in various climates, but are largely confined to the cold temperate regions where the soil is physically or physiologically dry and the shortness of the warm season prevents deciduous trees from becoming dominant. The ground cover consists largely of perennial plants. Many animals that live on the surface of the ground are more or less permanent inhabitants of coniferous forests. Among these moose, caribou, grizzly bear, wolverine, lynx, weasel, mink, otter, grouse, etc. are characteristic in North America (Shelford & Olson 1935). Blake (1926) has compared coniferous and deciduous forests of North America, from tundra formations to hardwood forests. Though conditions in different types of forests are rather similar the biotas may be quite distinctive. Blake found only 4.5 per cent of the animals, all nonpredominants, were common to both coniferous and deciduous forests. Coniferous forests in which soil cover has been continually burned over are modified, probably chiefly because many soil animals are destroyed (Heyward & Tissot 1936). In an unburned area 90 per cent of species of animals in litter were mites. Living among the foliage (Fasciation 1) in pine forests are chickadees, jays, crossbills, and other characteristic animals. Mites, beetles, ants, spiders and porcupines climb about among the branches (Fasciation 2); the red squirrel is pursued throughout its range by its chief enemy, the pine marten. Pine trees support many boring beetles that work in bark or wood (Fasciation 3). Woodpeckers, in turn, hunt these insects.

Consociation *a*(2). Deciduous Dicotyledonous Forests

Deciduous dicotyledonous forests are largely in temperate regions where there is a resting period during cold weather. Foliage may be present on the trees for 5–8 months, but during the remainder of the year the limbs are usually bare. The herbs growing on the forest floor are mostly tall, and such epiphytes as occur are mostly mosses and lichens. Fungi commonly grow in the soil or in deadwood. Trees of the same species are often gregarious, and there are several types of forest (beech, oak, birch, etc.) that depend on climate, soil, and other factors. In the broad-leaved forests of temperate regions phytophagous insects are more or less prevalent and are usually distributed according to their food preferences (Fasciation 1). These are

pursued by predaceous animals: spiders, assassin bugs, ants, warblers, flycatchers, vireos, etc. Some treetop animals move about actively; others spend their entire life cycle on one leaf (De Grysse 1934). Among the branches (Fasciation 2) crows, herons, and other birds find safe nesting sites. Scale insects and aphids attach themselves to the trunks or branches of the trees. Spiders, beetles, and predaceous insects feed on these and, in turn, furnish food for such birds as warblers and creepers.



FIG. 102.—Southern cypress, tupelo gum, and other swamp-hardwood trees in Southern United States. (*From Mattoon* 1936.)

The red squirrel of coniferous forests is replaced in broad-leaved forests by the gray and fox squirrels. In the United States the wood rat (Neotoma) also builds great nests of sticks, either in trees or on the ground. It lives in colonies in these and ranges through forests (English 1923). The deer mouse (Peromyscus), so characteristic of forest areas, is greatly influenced by humidity in its distribution (Chenoweth 1917). In bark and wood (Fasciation 3) are to be found boring insects, woodpeckers, mice, raccoons, and other characteristic animals. During the resting season many of the invertebrates (except those that bore in wood) are hibernating, or estivating, and the same is true of certain mammals. The birds, mammals, and invertebrates

that remain active through the resting season subsist largely on stores of nuts, wood, buds, animals, or other foods. Both resting and active animals may change to different strata at various seasons (Davidson 1930, Park 1930). In low-lying wet areas in Northern climates, characteristic animals are associated with tamarack and other trees; in the South, cypress and tupelo (Fig. 102) shelter certain frogs, water moccasins, racoons, deer, and other animals.

CONSOCIATION *a*(3). EVERGREEN DICOTYLEDONOUS FORESTS

Conditions in Rain Forests.—The necessary conditions for an evergreen dicotyledonous forest are moisture (60–80 in. of rainfall per annum) and high temperature. Such forests are characteristic of the moist parts of the tropics and certain temperate portions of the Southern Hemisphere. The edge of the tropical forest is overgrown with a tangle of lianas, epiphytes, ferns, arums, cannas, etc., but the interior may be rather bare and dark on account of the density of the foliage and the height of the trees. Epiphytes often cover the branches. Though many species are intermingled, the interior of the forest is often monotonous and gloomy. Palm forests, on the other hand, give comparatively little shade and are usually properly to be classified as savannas. Allee (1926) has made careful observations of barometric pressure, evaporation, air movement, temperature, and light in the Panamanian forest. "The series of measurements shows that the lower tropical rain forest presents remarkably constant environmental conditions." In regions where illumination did not reach 8 ft.-candles during the day there was "a marked reduction in number of species and individuals" (Allee 1926*a*). The treetops were more thinly populated than the forest floor. In Guiana Carter (1934) observed that in the shade of an undisturbed rain forest, light was only 0.8–0.2 per cent of sunlight in the open.

Animals in Rain Forests.—Certain of the animals in a tropical forest live in the treetops (Fasciation 1) and are highly adapted to life in such situations. Beetles, butterflies, parrots, toucans, sunbirds, hummingbirds, sloths, etc., feed on leaves, fruits, and flowers. There are also predaceous species, such as mantids, tree frogs, slender tree snakes, and hawks. Allee (1931) has given a summary of the ecology of animals in American rain

forests. He states that homeotherms tend to be smaller and poikilotherms larger than in cooler climates; life cycles are shorter and more rapid; ants are abundant, and certain animals are



FIG. 103.—In the Caribbean National Forest on the mountain slopes of Puerto Rico. (*From Mattoon* 1936.)

adapted to feed on them exclusively; fruit-eating bats and nectar- and pollen-eating birds are largely confined to the tropics; insect-pollinated flowers are relatively common; struggle for

existence is among living animals rather than with environmental conditions; flocks of birds composed of various species are common; trees of various species are mixed together, there are seldom "pure stands"; there is often a lack of seasonal periodicity; daily cycles are usually clearly defined; few eggs usually are laid by birds, short summer days perhaps making it more difficult to feed large broods; lack of horizontal air currents under dense forests is unfavorable for animals that hunt by scent; hearing is often used by forest animals (many are noisy); ungulates are small and fitted to squeeze through underbush (pig) or large and able to break down vegetation (elephant); arboreal animals have such adaptations for climbing as claws, hooks, opposable toes, sucking pads, prehensile tails; climbing animals are usually small; some have ability to fly or sail; there are relatively few animals in the depths of a forest, but many along the margins (savannas are more densely populated than thick forests); in many groups a forest serves as a refuge for primitive types that cannot survive in the open. In Africa, Boetticher (1933) states that more primitive types of pigs dwell in forests; they have bright-colored coats, whereas species that dwell on the veldt or savanna have dull colors. In Panama, Park (1938) has studied diurnal periodicity of several tropical animals. They fall rather clearly into two groups, day and night.

The high humidity in the forest permits many animals that are usually associated with the surface or subterranean strata in other habitats to wander about over the trunks and branches (Fasciation 2). Hence, lizards, snakes, and monkeys are often associated with snails, isopods, and amphipods. Annandale (1907) has described an earthworm that is abundant in an Indian forest, where it crawls about over the trunks of trees at night. There is the usual society of woodworkers in the tropical forest: boring insects (especially termites), woodpeckers, rodents, etc.

Types of Evergreen Forests.—Ruthven (1922) divides the forest in Colombia into the following zones and cites characteristic animals that occur in each:

Below 2200 feet:

Ravine forest—large trees growing up from bottoms of ravines; ground litter developed somewhat; drier than above 2200 feet.

Scrub forest—occurring in clumps on plains and on ridges; little shade, little ground litter; two strata, arboreal and ground.

Above 2200 feet:

Tropical rain forest—progressively wetter at higher altitudes; large trees, dense shade, deep ground litter.

Cloud forest—like last, but cooler and more humid; bromeliads more important.

In Tanganyika Moreau (1935) finds six types of forests at different altitudes: lowland evergreen, intermediate evergreen, intermediate dry evergreen, highland evergreen, cedar, and



Fig. 104.—Bromeliads and other epiphytes on trees, Colombia. (*By A. G. Ruthven.*)

highland-evergreen scrub. In these, birds are segregated according to stata and foods.

Epiphytes.—Ruthven (1922) points out that above 4,500 ft. bromeliads, both epiphytic and ground-dwelling, become more abundant and important as habitats for animals. Scott (1912) and Picado (1913) have discussed the relations of forest bromeliads. The former compares the habitats that these plants furnish for animals to a swamp but points out that there are differences, in that those in bromeliads are arboreal, have peculiar conditions of lighting, and are restricted in area. Their water

reservoirs are supplied by both rain and dew and contain water when swamps are dried up. Between the leaves of the epiphytes are to be found dragonfly nymphs; beetle, moth, fly, and mosquito larvae; frogs' eggs and tadpoles; planarians, earthworms, snails, isopods, amphipods, ants, cockroaches, locustids, earwigs, centipedes, scorpions, spiders, tree frogs, and snakes. Scott (1912) also found dytiscids and many other animals among the bases of palm and pandanus leaves in the Seychelles. Some of



FIG. 105.—A bromeliad, Colombia. (*By A. G. Ruthven.*)

the cockroaches and beetles that live between the leaves of such plants are remarkably flat.

Savannas.—Where trees are interspersed with areas of herbs and shrubs there are usually more animals and greater variety than on monotonous stretches of forest or grassland. In Africa savannas are favorite resorts for many of the game animals. Tall guinea grass furnishes food and shelter for ruminants, rodents, and ground birds; the trees are especially useful during the dry season, when the grass is usually burned over by natives in order to facilitate hunting. In South America there are great stretches of savanna which are populated by characteristic animals. Plovers and anteaters remain on the ground and belong more to grasslands; cuckoos and parrots belong to shrubs

and trees. Judged by the distribution of reptiles and amphibians, certain savannas in Central America are of recent origin and apparently have been produced by the clearing of forests. In areas covered by trees there are many characteristic animals, but few occupy the grasslands (Ruthven 1913).

Association *b*. Shrubs

Shrubs are usually prevalent in areas where it is too dry or too cold on account of high latitude or altitude to support trees, but where conditions are favorable enough to support larger plants than grasses. Shrubs also often occur in zones of transition, along the margins of swamps or forests. As a habitat for animals they differ from trees in being close to the ground. Morse (1904) has pointed out that the typical orthopterans that live in forests are provided with long, slender wings for flying from tree to tree or across open spaces, but those that live in thickets of shrubs are frequently wingless and adapted to hopping or clinging, probably because flight is difficult. A walking stick is characteristic of shrubs. When disturbed, it may go into a death feint and remain motionless for a long period; or if it is knocked to the ground by a passing animal, it may easily climb back among the foliage. Spiders and other animals that visit the ground at intervals are more numerous than those among trees. The lack of large open spaces among shrubs makes it difficult for large predaceous animals to pursue their prey; robberflies and orb-weaving spiders are more common in such situations than hawks. Certain birds, like the cuckoo, trogon, cardinal, catbird, and brown thrasher, frequent thickets.

Some of the animals (tree frog, katydid) that are found in forests may also live among the foliage (Fasciation 1) of thickets. Phytophagous insects, such as chrysomelid beetles, leaf miners, and aphids, are apt to be more abundant and varied than in forests; and their enemies, the ichneumons, reduviids, asilids, and aphis lions, are also prevalent. Among the branches (Fasciation 2) insectivorous birds are characteristic animals. Forbes and Gross (1922) found more birds in orchards than in any other habitat in Illinois. Borers (Fasciation 3) are not so prevalent as in forests, probably because the small volume of woody structures does not offer such stable habitats.

Association c. Low Plants

Grasslands.—Plains, prairies, pampas, steppes, meadows, and tundras are alike in supporting low vegetation. Where there is considerable moisture, composites and other herbs may rival or exceed grasses in numbers; but where it is drier, the opposite is usually true. In Alaska, Dice (1920) has described hummocks of tough grass which occur in low situations where the drainage is poor. These may be several feet high and are frequented by ptarmigan, shrew, weasel, mink, lemming, vole, moose, and other animals in a country that otherwise affords little shelter. Waller (1918) in discussing the regions of North America says that the plains begin where humidity falls below 60 per cent and are characterized by the presence of pronghorn antelope; prairies occur farther east where the striped ground squirrel is found. Ruthven (1908) maintains that few species are wholly confined to the prairies or plains but that each has certain animals that are distinctive. On the prairie are the prairie horned lark and nighthawk; on the plains, the pallid horned lark and Sennet nighthawk. The prairie also supports certain animals that properly belong to the eastern forest region, and the plains harbor animals that are perhaps better adapted to life in the prairie. In localities where there is marked aridity there are often two resting seasons—during a cold winter and a hot summer. In moist meadows there is usually one period of rest, in winter. In Illinois, Adams (1915) found that prairie was a mosaic of societies. He describes various types of prairie communities: swamp prairie, cottonwood, swamp grass, low prairie, upland prairie, Solidago, dry prairie, and milkweed, each with characteristic species of associated plants and animals. These range from wet swampy areas to dry uplands. Sandy soil and good drainage produce a dry prairie; loam and good drainage result in a black-soil prairie; poor drainage leads to a wet prairie. Though climate in the Western United States has varied greatly in the past, since the North American continent has had its present form the Mississippi Valley probably has been a region of transition from forest on the east to steppe and desert on the west. Lately cultivation and overgrazing have destroyed prairie-soil covers; destructive dust storms have resulted (Clements & Chaney 1936). The roots of prairie plants form a continuous mat below the surface;

when this is destroyed there is no impediment to erosion (Weaver & Harmon 1935). In the mountains of North Carolina there are "balds," or prairie grassland areas, in the midst of forests. Men and other animals perhaps have contributed to the formation and maintenance of these.

Characteristic Grassland Animals.—The low vegetation in grass and herb association gives little protection from light, heat, and cold. Hence many animals remain underground part of the



FIG. 106.—Chimney of a burrowing crayfish. (*By Hankinson, from Adams* 1915.)

time and are often nocturnal or crepuscular. There are no strata above ground except those on or within plants. Animals such as prairie crayfishes (Fig. 106) frequent wet areas but can endure drought. Wet seasons may bring about an increase not only in such animals but in the total population, because vegetation is more luxuriant (Hendrickson 1935). In drier prairies the dominant animals are insects (Vestal 1913). On account of lack of available lime there are usually few snails; millipedes and earthworms are rare. Spiders, collembolans, termites, aphids and antlions, dragonflies (many miles from aquatic habitats), locusts, carabids, and other predaceous beetles, dipterons, and hymenop-

terans may be more or less common. Snakes and lizards are usually more common than birds. There may be mammals, such as the antelope, bison, buffalo, ground squirrel, vizcacha, skunk, puma, mouse, and rat.

In the tropics dry grass and forb stretches may be interspersed with trees and thus form savannas. Here such animals as stone curlews and anteaters are at home. Near the poles the



FIG. 107.—Nest of meadowlark containing two eggs of owner and three of cowbirds. (*From Forbes & Gross* 1922.)

tundra is inhabited by reindeer, foxes, lemmings, and other animals. In temperate regions that have enough moisture to support meadows, thickets, or forests, areas are often converted by man into pastures, parks, or gardens. Sometimes meadows border bodies of water which inundate them at times, but they may also be far from water at high altitudes or, in any fairly moist region, may occur where continual grazing keeps trees and tall shrubs from gaining a foothold. They are populated chiefly by herbivorous insects, rodents, and other mammals, with the predaceous animals that feed upon them. Mowing and grazing do not kill out certain grasses but make them form denser

growths. Vestal (1913) says that some species of grasshoppers are more characteristic of cultivated than of natural grasslands. Harshberger (1923) has proposed the term "hemerecology" for the ecology of the areas modified by man. Prairie animals as a group are not highly adapted, and many of them occur on adjacent areas of different types. "Environmental conditions are not either extensive or intensive enough to mold forms into a peculiar fauna" (Ruthven 1908). Perhaps prairie dogs (Cynomys; Fig. 108) are as characteristic as any other animals on the dry grasslands in the Western United States. Several varieties of them occur in different regions (Hollister 1916).



FIG. 108.—Plains prairie dog, *Cynomys ludovicianus*. (*From Merriam* 1902.)

Adaptations of Grassland Animals.—Vestal (1919) has pointed out that many of the insects that live in bunch grass are typically sedentary but found that the "interstitial" animals, which frequent the spaces between vegetation, are usually swift and predaceous. Many of the larger herbivores (jack rabbit, antelope, mice) are swift, and the same is true of certain of the carnivores (foxes) that pursue them. Morse (1904) stressed the fact that the best flyers among locusts are found in open fields, where wide-open areas make dispersal and escape from enemies easy, especially through the aid of winds. Collins (1922) states that the vision of prairie mammals is commonly panoramic and good in either dim or bright light. The olfactory and visual senses are keen and serve to give warning to prey or to notify predators of the presence of food. Jack rabbits and some other animals have very large ears. Predatory animals commonly have a considerable degree of bifocal vision and often see better in dim light than their prey. Animals that depend on speed for

escaping usually have the eyes protruding prominently from the head.

Density of Population in Grasslands.—When conditions are favorable many animals may be present. Wolcott (1918) after studying the Illinois prairie (as represented by city lots) estimated that there were 1,756,932–1,009,104 insects per acre and that other animals present in the subterranean, surface, and vegetation strata varied from 3,700,048–2,422,760 per acre. In the Illinois sand dunes, Sanders and Shelford (1922) estimated that there were about 84,000 animals per acre. Saunders (1907) gives the following estimates of the average number of acres required by each pair of breeding birds in Montana: grass meadow, 7.5; cinquefoil brush, 7.5; cottonwood grove, 0.53; stream border, 0.45; cattail slough, 0.67. These figures indicate that grasses and herbs contain less food for nestling birds than groves or areas near aquatic habitats. Water in the form of lakes, ponds, pools, or streams is not necessary, however, for many herb-inhabiting animals. Some grasshoppers will die of thirst when they have access to a dish of water but will not do so when drops are sprinkled about that can be sucked off surfaces like dew (Snyder 1904). Many prairie animals can get along without drinking at all. Prairie birds are not so numerous as those in savannas (Forbes & Gross 1922). Some species, such as horned larks, sharp-tailed grouse, and meadowlarks, flourish in open grasslands; others (quail, etc.) do better when shelter in the form of shrubs or tall herbs is available (Sumner 1933). The number of young jack rabbits produced in Southern Arizona each year is correlated with the amount of precipitation, which of course influences vegetation (Vorhies & Taylor 1933). Insects also emerge from resting states in greater numbers after rains (Wilbur & Sabrosky 1936).

Food of Grassland Animals.—Animals that feed on the low vegetation that grows in open places have the advantage of the unobstructed view that enables them to observe enemies but must be able to endure the lean seasons, when food is greatly decreased or wholly absent on account of cold or drought. The reindeer (Hadwen & Palmer 1922) is perhaps as well adjusted to life in open places as any large animal. It feeds in the summer on windswept areas near the sea, where it escapes to some extent from mosquitoes and warble flies and is able to obtain salt.

In winter it paws through the snow and feeds on a variety of mosses, lichens, and other plants. The lemmings and voles remain active through cold seasons in tunnels beneath the snow. Many prairie animals lay up stores which are often protected by being placed in underground chambers. Pocket gophers and certain other rodents have cheek pouches which they use for transporting food. Ossendowski (1922) gives an interesting account of a rodent that he encountered in Mongolia. This was a gigantic black rat which lived in colonies of one or two hundred. It is said to mow grass with its teeth and dry it. A mound of loose earth about a foot high is then prepared near the mouth of the burrow, and the hay is carefully piled on it. About four stakes are pushed through the hay into the loose earth below, and the whole mass is then bound together with grass so as to prevent it from blowing away. Quite a number of prairie insects depend for food and shelter on the dung of larger animals. In a pasture in New Jersey Wilson (1932) found 43 species of beetles and 64 species of flies associated with sheep dung. Prairie animals often become pests in garden or field crops (Adams 1916). About 4 per cent of the food of a Philippine seed-eating weaver bird consists of rice (Manuel 1935). Even mowing or pasturage exerts a profound influence on the species of rodents and grasshoppers present (Rubtsov 1932, Phillips 1936). Every plant association has its characteristic grasshopper community, determined largely by food preferences, but different types of insects vary with seasons (Carpenter 1937, Fletcher 1930).

Enemies of Grassland Animals.—Enemies that beset the animals of prairies and similar habitats are usually swift and powerful. Many of the rodents are gregarious and commonly give alarm notes that warn of the approach of danger. On the pampas in Argentina the vizcachas are caught by the puma; a fox often usurps one of their burrows and devours their young (Hudson 1922). The prairie dog of the western plains of the United States is eaten, especially while young, by coyotes, owls, and rattlesnakes. Bailey (1893) and Hollister (1916) state that the chief enemies of the ground squirrels and prairie dogs are (1) hawks and owls, which pursue them aboveground; (2) the badger, which digs out their burrows; and (3) the bull snake, which also catches them underground. The reindeer is attacked by the bear, wolf, lynx, wolverine, and eagle. It is peculiar

among deer in that horns are present on both sexes. Voles are most active when enemies are least active—at dawn and dusk. The home range of each vole is seldom more than a fifteenth of

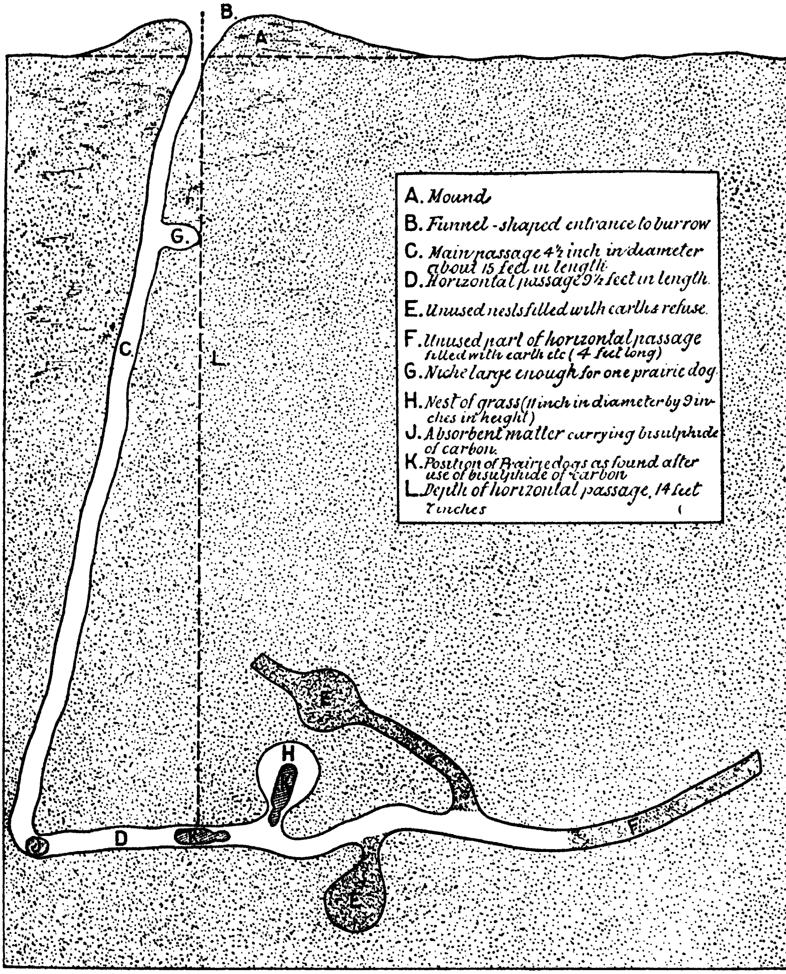


Fig. 109.—Plan of a prairie-dog hole, after fumigation with carbon disulfide. (*From Merriam* 1902).

an acre, but an individual will return home if moved 100–250 yd. from the area with which it is familiar (Hamilton 1937*a*). In its own territory, it knows hiding places and can thus better escape.

Burrowing and Nonburrowing Animals of Grasslands.—Though many prairie animals have more or less permanent homes in holes in the ground, there are many that do not do so. Certain rodents (prairie dog, ground squirrel) always live in burrows and are never seen far from them. Hudson (1922) says that bank swallows dig their holes in the sides of the large entrances to vizcacha burrows and are dependent on the rodents for nesting sites. The vizcacha is highly adapted to life in burrows, even having a special claw on the hind foot which serves as a comb for removing parasites. Some prairie animals have permanent holes which serve as dens but spend more time in them during the breeding season than at other times (coyote, trapdoor spiders). Other animals commonly use burrows that they do not dig themselves (snakes, owls). Jack rabbits, many mice, insects, grouse, and other animals do not dig burrows but crouch among vegetation and are well concealed by their coloration.

Strata on Grasslands.—The strata above the ground are not so sharply defined as those among taller vegetation. Animals that are subterranean or perhaps properly classified in the surface stratum may have relations with the highest parts of the vegetation. Most of the larger animals, in fact, belong to the surface stratum, yet they are more or less characteristic of situations where low vegetation occurs. Both tree squirrels and prairie dogs are dependent on vegetation and often journey over the surface of the ground; but the former are found in forests, and the latter in prairies. About the only type of fasciation that applies to the small animals that live among or in low vegetation is that which depends upon whether animals live on the outside of or within plants.

Tundra.—The grasses, sedges, and forbs that largely make up the plant constituents of tundra societies tend to be dwarfed and often grow in dense patches. Tundra occurs north of, and above, coniferous forests. Characteristic animals are caribou, musk ox, arctic fox, arctic hare, ptarmigan, snow bunting, lemming, etc. Many of these animals change coats with the seasons and are otherwise adapted to life in arctic or alpine regions.

Association *d*. Deserts

Conditions in Deserts.—Deserts are not wholly due to the extreme condition of any one climatic factor but are primarily

brought about by continual lack of water which, though it may be present in considerable amounts during certain seasons or years, is erratic in its distribution and always meager. In the Sonoran Desert, west of Tucson, Ariz., rainfall varies with elevation: below 1,000 ft., 4.19 in.; 1,000–2,000 ft., 8.1 in.; 2,000–3,000 ft., 11.03 in.; above 3,000 ft., 25+ in. (Mallery 1936, 1936*a*).

> In brief, a desert climax is one marked by the absence of forest or grassland, a critical deficit in rainfall, a high potential evaporation caused by excessive heat and often by high winds also. . . . Deserts usually lie in direct contact with grassland rather than woodland or forest (Clements 1936*b*).

The large deserts are mostly just north or south of the equator. Some of these occupy the beds of ancient seas. Some, though they contain more or less water, are physiologically dry on account of the presence of large amounts of salts. These are "alkali" deserts. The low relative humidity in deserts is associated with lack of clouds. The days are bright and sunny, with a correspondingly great action from all the wave lengths of light. Deserts may occur in connection with any type of earth surface, but hard soils are least favorable for animals because they do not, like sand, give an opportunity for burrowers to escape unfavorable conditions. The absence of atmospheric moisture allows heat to radiate quickly from the earth. The nights are usually cold and thus are in sharp contrast to the hot days. There is little or no shade to afford shelter from the intense heat and light. The surface of the soil may reach 75–85°C. and at midday is often 20°C. hotter than the atmosphere in the shade. Most animals hide away during the middle of the day, and many are crepuscular or nocturnal.

Desert Plants.—In deserts there may be thickets of shrubs (Spalding 1910) but, as a rule, there is little opportunity for animals to pass directly from plant to plant. Many animals spend much of their time on or below the surface of the soil. The vegetation consists largely of taprooted perennials and thick-stemmed plants which have various adaptations for conserving water. For a short period after rains there may be annual plants, which at other seasons are in nonvegetative states (seeds, etc.). The soil of deserts is often rich in plant nutriment on account of

the salts left by water that is drawn up from the subsoil and evaporates from the surface, but such food is largely unavailable on account of lack of water to dissolve it. Desert plants, though differing more or less from each other, have a characteristic aspect. Dense woody structures, thorns, bitter or saline saps, dwarfs, rosettes, brief life histories, rolling habits, hygrochasy, enlarged green stems, and absence of leaves are common adaptations. By such peculiarities water is conserved, growth takes place rapidly during the short favorable season, the attacks of vegetarian animals are prevented to some extent, and, in general, the severe conditions of life are better endured. Rodents often keep desert plants from attaining maximum development by burrowing under and gnawing away their roots (Grinnell 1932, Kashkarov & Kurbatov 1930).

Adaptations to Lack of Water.—There are many animals that are especially fitted for life in deserts by the presence of particular racial traits. Lizards, kangaroo rats, sand grouse, road runners, gazelles, and camels are typical desert animals. They show adaptation—often to a remarkable degree—to desert life. Perhaps the chief difficulty among desert animals is to obtain and retain water. Some make frequent journeys to sources of water; some drink water but can remain active for considerable periods without it; some can exist without water, except that which they obtain in their food. Jerboas and other desert rodents can exist for months without water, except that obtained from dry seeds and vegetation (Buxton 1923, Grinnell 1926, Kashkarov & Kurbatov 1930, Sumner 1925). Desert snails have epiphragms and secretions that prevent water loss during dry periods (Mazek-Fialla 1934). Desert frogs, and even tadpoles, absorb much water during rains and then remain underground much of the time in order to retain it. The nocturnal habits of animals expose them to evaporation in the atmosphere when it is least effective as a drying agent. Some animals plug up the mouths of their burrows during the day. Reptiles and birds conserve water by excreting uric acid. Some desert animals are active for brief periods during the year when water and food are available. Buxton (1923) states that 50 species of protozoans were raised from soil after 8 months of drought. Not only invertebrates but amphibians, reptiles, and mammals may thus remain dormant. Buxton (1921) points out that there is

concentration in time and space: animals are abundant and active after spring rains, and few insect imagoes are seen in the hottest season; more animals are present among and beneath vegetation and where caves furnish shelter than in open spaces. Animals in arid grassland areas may change their habits markedly during periods of drought (Marais 1915) but of course do not become desert animals at once and for the most part die (Van Cleave 1931). But even in the Sahara some aquatic relict animals have persisted for long ages and today live in isolated pools (Seurat 1932). A kangaroo rat soon drowns if placed in water. It has no ability to swim, and its fur quickly becomes wet (Grinnell 1922).

Protective Adaptations of Desert Animals.—Most desert animals are colored so that they are not easily seen and commonly show the dull browns and grays that are characteristic of the environment (Dice & Blossom 1937, Sumner 1925). Many of them are very swift. Lizards that run on sandy areas may have fringes along the toes which aid their progress; the camels also have broad, soft pads on their feet. A desert cat in Turmenistan has wide fur-covered soles and runs easily over hot desert sands (Bil'kevich 1934). The rodents tend to have toes that are short, compact, and often reduced in number. Their limbs are generally long and slender, and the hind pair are often fitted for leaping. A number of desert animals are not only speedy but take an erratic course, which tends to confuse their pursuers. Among rodents such animals often have a long tail which helps in balancing (jerboa, kangaroo rat, etc.). The animals that have long legs and are able to stretch upward are easily able to keep a lookout for enemies. Nocturnal animals especially are often provided with large ears and an acute sense of hearing. Some desert animals are solitary (the kangaroo rat will not tolerate another individual in its burrow), but others are quite gregarious (the huanaco grazes in little herds, with one individual continually serving as a sentinel; Hudson 1892). Predaceous animals, as on prairies, have unusual adaptations which enable them to capture their prey. The badger digs animals out of their retreats; the swift depends on its speed; the owl approaches swiftly and stealthily and has very acute vision, especially in light of low intensity. Animals that burrow escape from heat, cold, evaporation, and certain enemies. Some of them have the

nostrils protected by special valves, and the eyes and ears are likewise often shielded. Some lizards have a transparent disk in the eyelid and are thus able to see when the eye is closed (Gadow 1913). The dust and alkali in deserts would probably be injurious to certain rodents if it were not for the oily secretions on the fur (Vorhies & Taylor 1922). Kangaroo rats occupy definitely spaced areas throughout deserts, and they guard these jealously from other rodents. They live in complicated burrows which have several exits. When pursued by their chief enemies, coyotes and owls, they dash out and leap quickly to other refuges (Grinnell 1932).



FIG. 110.—Banner-tailed kangaroo rat, *Dipodomys spectabilis spectabilis* Merriam. (*From Vorhies & Taylor* 1922.)

Adaptations to High Temperatures and Strong Light.—Some desert animals are able to endure very high temperatures, but most of them avoid the light and heat of the meridional sun. Buxton (1923) cites beetles and lizards that sit without apparent discomfort on rocks too hot for the human hand. The harvester ant in Texas always builds its nests in open places without shade and does not work on cloudy days. Wheeler (1911) says that it works through the middle of the day when the temperature of the soil is below 60°C. The eggs of the ostrich may be left in the sun without injury, but some birds cover theirs with sand. Certain desert leaf hoppers are orbicular, flat, and short winged. They have long slender legs which hold them high above the hot soil as they move about (Hartzell 1921). Lizards burrow at night to avoid low temperatures and are inactive throughout cold seasons (Gilver 1922). They appear

to have little toleration for high temperatures but escape them by burrowing or climbing to elevated situations above the hot surface of the soil (Kashkarov & Kurbatov 1930, Mosaur 1936, Sumner 1925). Some nocturnal animals (bats, owls) seek refuge in caves during the day. Vorhies and Taylor (1922) note the fact that the kangaroo rat escapes the attacks of warble flies by its strictly nocturnal habits.

Reproduction in Deserts.—Desert animals on the whole produce few offspring. They are well adjusted to environmental conditions and tend to live long lives rather than multiply rapidly. This, of course, is not true of some animals, such as certain insects and mice, which multiply rapidly with the increase of vegetation after rains. Desert birds usually breed early each year, before temperatures are high. The giant kangaroo rat breeds when vegetation is most actively growing (Grinnell 1932).

Food of Desert Animals.—The food of desert animals is related to the scarcity of water and the short growing season for vegetation. Wasps, bats, many birds, and some other desert animals visit bodies of water and drink at frequent intervals. The sand grouse not only leaves its nest to obtain water but carries a supply on its breast feathers for its young (Buxton 1923). The ostrich, giraffe, eland, pocket gopher, and grasshopper mouse get along without water but drink when it is available. Pocket mice eat dew and snow but probably do not drink (Bailey 1923). Some desert beetles also eat dew off plants. A camel can do without water for 8 to 10 days while subsisting on dry food and, if supplied with green vegetation, for 2 months. The mule deer and mountain goat get water from vegetation and never go near water to drink. The pronghorn antelope and jack rabbit eat cactus pulp (78 per cent water) and other succulent plants. The jerboa, certain ground squirrels, addax, oryx, and gazelle always go without water and are able to subsist for long periods on dry vegetation. Some carnivorous animals depend largely on insects and vertebrate prey for their water supply. In the Kara Kum desert animal life is "grouped around seven food centers": (1) sedges and grasses, (2) shrubs, (3) insects, (4) lizards, (5) rodents, (6) dung, and (7) water holes (Kashkarov & Kurbatov 1930). One ground squirrel makes stacks of hay and pins them down with pegs to keep them from being blown away by strong winds.

Food Storers.—Several animals that frequent deserts store food during seasons of plenty. The banner-tailed kangaroo rat collects vegetable food, principally the seeds of grasses, from April to November, and larders examined by Vorhies and Taylor (1922) contained 5–5,750 g. The desert kangaroo rat does not store food but steals from its more provident relative, which kills the thief whenever it finds it in its burrows. The Texas harvest ant carefully selects seeds off the ground and stores them in underground chambers; the Florida harvester climbs up on plants and pick off seeds. Both species husk their crops within the nest and carry out the refuse to midden piles aboveground. It is doubtful if either of these ants plants seeds and raises crops; they are foragers and storers (McCook 1879). Mann (1913) says:

> The harvesting ants are descended from insectivorous forms, which have taken up the grain-storing habit as an adaptation to life in the desert, in steppes, etc., where, during parts of the year, insect food is scarce. Seeds can be stored and kept, which is not true of insect food.

Honey ants collect honey from aphids (Buxton 1923) and galls (McCook 1882) and keep it in peculiar workers which serve as living bottles.

Cliffs, Ravines, and Canyons.—Precipitous rocky faces are barren surfaces, or local deserts. They do not support much vegetation and therefore furnish little food but are safe retreats for animals that seek food elsewhere. Flying animals such as swallows, hawks, eagles, wasps, and other insects find safe nesting sites on such situations and hunt over neighboring forest, prairie, and desert areas. Some nonflying animals also have dens in them and forage in near-by areas. Ants and spiders are characteristic arthropods. Cliff rats (Neotoma) build nests and make great midden piles in crevices. They are also found in caves (Newcombe 1930).

FORMATION 3. AERIAL HABITATS

Use of Air by Plants and Animals.—Historically, the air was the last of the nonaquatic habitats to be invaded by animals. Lull (1906) states that in the evolution of vertebrates volant adaptations have occurred seventeen times—ten times for gliding and seven for flying. He also affirms that the ability to glide,

and probably also to fly, has commonly been associated with ancestral adaptation to arboreal life. The ability to sail or fly through the air makes greater speed possible than can be attained by cursorial animals. It is useful for reaching inaccessible situations, escaping from enemies, seeking food, distributing species, migrating from unfavorable to favorable localities, etc. Of course, there is no animal that lives permanently in the air without contact with solid objects, but many animals spend most of their active lives there. The swifts even pick off twigs and in part build their nests while fluttering on the wing; a buzzard may soar for hours without flapping its wings. By exposing culture media and using sticky surfaces or special traps on airplanes the presence of plants and animals at various altitudes has been investigated. Living fungus spores and bacteria decrease gradually at higher altitudes but occur in considerable numbers at least as high as 3,000 ft. (Mac Quiddy 1935). Ballooning larvae of gypsy moths ascend to altitudes of 2,000 ft. or more (Collins & Baker 1934).

Types of Adjustment to Aerial Life.—All animals that move through the air are heavier than the medium that surrounds them and hence lack the help of the buoyancy that keeps many aquatic animals near the surface. The ability of animals to remain in the air depends largely on (1) the ratio of horizontal surface exposed to weight and (2) the rate of movement. Ballooning spiders have no active means of progression and therefore depend on winds. The Javan tree frog, Draco, and flying squirrels volplane down from elevations and after attaining a certain velocity may even rise somewhat at the end of a journey. Animals that progress through air or maintain themselves at a certain level by flapping wings have to do work continually, but those which have attained ability to soar carry on such activities with little effort.

Adaptations for Flight.—Aerial animals are usually light, active, keen of vision, have smooth and slender contours, possess rigid and at the same time flexible bodies and wide surfaces. The adaptations of such animals have been described in detail by Hankin (1920). May-fly nymphs gulp air into their bodies to inflate themselves and thus create enough pressure to burst their skins when they are ready to shed them. Adult May flies carry on similar activities as an aid to flight (Morgan 1913). There

has been considerable dispute as to how aerial animals maintain themselves in the air. It is easy to see how a wind carries, and even elevates, a mass of web like the balloon of a migrating spider. Gliding downward from elevations is readily understandable. It is also easy to see how a bat, bird, or insect can hold itself in the air by flapping its wings. But how birds and insects are able to soar in the air for considerable periods of time without beating the air with their wings is harder to explain. Hankin has pointed out that soarers have longitudinal ridges on the under surface of their wings and that animals that fly by flapping (owls, bats) lack these. Townsend (1909), Beetham (1912), and Hankin (1915). have given extensive descriptions of different types of flight in various animals, describing methods of starting, stopping, steering, balancing, etc. Some birds are not able to take off unless they can gain momentum by swimming or running; many birds are not very expert at what is perhaps the hardest task for all flyers—stopping. Long-legged, short-tailed birds use their legs as rudders while flying; birds with small feet fold them up while flying and steer with their tails. Long-winged birds and bats commonly move up and down by moving the tips of their wings.

Feeding in the Air.—Many animals feed largely or wholly in the air. Bats catch food with their sharp teeth, and Lucas (1897) states that struggling animals are covered over with a sticky oral secretion which prevents them from escaping. Goatsuckers and swifts feed on the wing and have a wide gape with bristles at the corners of the mouth which help in the capture of insects. Hawks and owls have spreading talons for the grasping of food on the wing; dragon- and robber-flies attain the same ends with their leg baskets.

Senses of Aerial Animals.—The high speed at which sailing and flying animals move makes good sense organs necessary. Vision is usually acute; touch and hearing are often developed to a high degree. Quickness of movement and excellent muscular coordination are characteristic. Bats are able to avoid obstacles without using their eyes. Blinded bats can fly about among wires without touching them. The hairs on their bodies are richly supplied with nerve endings and serve sensory functions. Hahn (1908) believes that bats perceive obstacles while flying by making high chirping sounds which are reflected back to their

ears from objects in their paths. Birds have large, protruding eyes which enable them to see and avoid obstacles. Bifocal vision is developed to a considerable degree in predaceous birds. The enormous eyes of a dragonfly cover most of the head, which is loosely pivoted on the body so that it can be turned nearly 180 degrees. Many flying animals have pronounced homing instincts and remarkable ability to return to particular spots or move in a certain direction without losing their way. Bats return after each foray to their accustomed retreats and do not emerge unless the weather is favorable. Birds have roosting places to which they return continually and are thus saved the trouble of seeking a new site each time that the sun goes down. Insects that have regular homes may return to them to sleep. A continual and accurate cognizance of the surroundings through the senses and a recognition of directions and relations are essential for animals that use the air as a highway.

Duration and Speed of Flight.—Animals that have heavy loads in proportion to their horizontal sustaining surfaces cannot make long flights, but those that are highly adapted may soar for hours with little effort and cover great stretches of territory. The "flying dragon," *Draco voltans*, is able to glide for a distance of 40–50 m. A flying fish can rise 5–7 m. above the surface of the ocean and usually does not cover more than 100–200 m. in a single flight, though in exceptional cases it may fly 500–800 m. A bird may ascend to an altitude of 2 km. and perhaps traverse a tenth of the circumference of the globe without stopping to rest (Coward 1912). The speed at which birds fly probably rarely exceeds 100, and most do not exceed 50 m.p.h. (Meinertzhagen 1921). Among the speediest of birds are: duck hawk (180 m.p.h.), golden eagle (120), vultures (89–110), swallow (106), canvasback duck (72), golden plover (70), and swift (68) (Andrews 1937).

Association *a*. Ballooning and Gliding Animals

Spiders and some insect larvae progress through the air with the aid of balloons of cobweb. They are largely confined to the surface of the soil and low vegetation except when they are traveling, and they balloon at infrequent intervals (Fasciation 1). Gliders are found among fishes, tree frogs, lizards, and mammals (Fasciation 2). They are all arboreal except the fishes, which

gain elevation by leaping out of the water. Flying fishes probably never flap their "wings." They attain momentum by vibrating their tails rapidly in water while their bodies are in the air, then volplane. They can make longer flights against winds than in quiet air. They usually remain in the air less than a minute, have good control over their course, and are able to change direction or elevation (Hubbs 1935).

Association *b*. Flying Animals

Flying animals may be differentiated into those that spend most of their time closely associated with the surface of the earth (Fasciation 1) and those that live most of their active life in the air (Fasciation 2). Grouse, ducks, geese, warblers, grasshoppers, and many other animals, though good flyers, use the air only as a highway in passing to and from roosts, feeding grounds, breeding places, etc. Predaceous animals, such as swifts, nighthawks, vultures, and dragonflies, are more or less continually in the air seeking food. They are not necessarily to be found above any particular terrestrial or aquatic habitat. Many such animals are able to soar.

APPENDIX I. ISLANDS

Plants on Oceanic Islands.—The animals that live on islands, especially oceanic islands, though dwelling in the same types of formations, associations, and fasciations that are found on continents, are often subjected to unusual conditions, both in the living and in the nonliving environment, on account of the limited area of the land mass that they inhabit and its isolation. The numbers of species of plants and animals on isolated islands are usually limited. Stewart (1915) points out that there are more species of ferns than of spermatophytes on the Galápagos Islands, probably because their small spores are readily carried by winds. Schimper (1903) states that there are fewer flowers pollinated by insects and fewer insects on islands.

> Both phenomena are to be attributed to strong winds, which on one hand lessen the number of insects and plants associated with them, and on the other hand favor anemophilous flowers.

MacCaughey (1917*a*) has emphasized the remarkable endemism of the plants of the Hawaiian Islands. Over 85 per cent of

the flowering plants are not found elsewhere. Endemism among the plants in other Pacific islands is as follows: Samoa 34, Tahiti 35, Fiji 53, New Zealand 75 per cent.

Animals on Islands.—Amphibians and mammals are usually absent from oceanic islands (Wallace 1912). This makes conditions peculiar. Habitats dominated in most parts of the earth



FIG. 111.—Bull seals waiting for cows to come to breed, on one of the Pribilof Islands. (*From Parker* 1917.)

by ubiquitous rodents or ruminants may be characterized by reptiles or other animals. Darwin (1859) said:

> The species of all kinds which inhabit oceanic islands are few in number compared with those on equal continental areas. . . . Oceanic islands are sometimes deficient in animals of certain whole classes, and their places are occupied by other classes: thus in the Galápagos Islands reptiles, and in New Zealand gigantic wingless birds, take or recently took, the place of mammals.

In some islands frogs, being introduced and not being kept down by natural enemies, have become a nuisance. Bats, certain birds, and insects are, of course, distributed more or less to all islands. There are often endemic and wingless birds and insects, however. These are adapted to insular life by being unable to fly; in fact, the power of flight might be detrimental because they could be swept out into the open sea and lost. Even such marine animals as corals are represented by few species on isolated islands (Crossland 1928, 1931). Marine molluscs (Tomlin 1934) and other invertebrates (Mumford 1936) show endemic

tendencies. Such endemism is even more pronounced among land invertebrates. On New Caledonia of 153 species of spiders 95 are endemic; also 64 per cent of ant species, a large percentage of snails and isopods, and 76.5 per cent of plants (Cockerell 1931). In Hawaii there apparently have been three invasions of Odonata at widely separated and different periods in the past, not continual additions to the fauna (Kennedy 1928*a*). On an island only sixty years old, Alfken (1930) found mostly aggressive and modern types of insects. On the Apostle Islands in Lake Superior all mammals that have become established are of types that do not hibernate and hence can emigrate from the mainland over ice (Jackson 1920). Islands along the coast of Alaska have probably been populated with plants and animals since Pleistocene time (Swarth 1936). There have been ardent advocates of the population of oceanic islands over land bridges (Scharff 1907, 1912), but Gulick (1932) believes that winds and currents, especially at times of hurricanes, have been more significant. Isolated islands often serve as sites for breeding colonies of animals such as seals (Fig. 111), other pinnipeds, pelicans, swans, and auks.

APPENDIX II. ANIMALS FREQUENTING STRUCTURES MADE BY MAN

Many buildings and other structures built by man are occupied by animals, and some species are largely confined to such situations. Bats, swallows, swifts, owls, woodpeckers, wasps, and bees find shelter and nesting sites in buildings but forage for food elsewhere. Predators and scavengers, like rats, mice, clothes moths, house lizards, centipedes, spiders, ants, mosquitoes, bedbugs, and fleas, find temporary or permanent homes in dwellings and also find food there. Some of these animals are very desirable companions for men; others are more or less pestiferous. In the Philippines every dwelling supports a few house lizards which scamper about the walls and do much good by destroying vermin. The cockroaches, ants, termites, and other insects that these lizards devour are not pleasant to have about.

Hobson and Mathews (1923) have published a very interesting account of the "Ecology of King's College Chapel." They divide the animals into (1) independent species, which find food out-

side the chapel; and (2) dependent species, which carry on all activities within the building. Pigeons, bats, and hibernating insects come and go; ticks, fleas, certain mites, and bird lice for the most part lurk in crevices during the day and come out at night to suck blood; Lepismas and the larvae of the beetles, flies, lepidopters, and fleas feed on feces or the bodies of dead animals; spiders, beetles, pseudoscorpions, and certain mites catch small animals and devour them.

Insects that infest stored foods include several hundred species.

CHAPTER XI

RELATIONS OF ANIMALS TO PLANTS

Though the vegetation of the earth was discussed in the last chapter as an important determiner of terrestrial habitats, it is proper to devote some space to the consideration of certain of the many special relations between plants and animals. The vegetation covering the earth exerts an important influence on climate and other features of particular localities. Changes in it often bring about profound alterations. For example, the denudation of forests has in some regions been the cause of frequent floods. A brief general discussion of the relationships between land animals and plants has been published by Taylor (1936) who considers disturbances of natural balances, foods, seed distribution, pollination, seed dispersal, protection, and other matters particularly concerned with beneficial and injurious species in relation to man.

Interdependence of Plants and Animals.—A plant and an animal are more or less interdependent, and the activities of one result in waste products that are necessary for the syntheses of the other. Photosynthesis, the process that gives rise to nearly all the organic food of plants and animals, requires carbon dioxide, which is, in turn, commonly liberated by the disintegration of organisms. Decay is usually brought about by bacteria and other fungi. All protoplasm forms carbon dioxide as a product of metabolism. Except for anaerobic organisms, both plant and animal protoplasms require a continual supply of oxygen for metabolism, and oxygen is an end product of photosynthesis. Carbon dioxide in large amounts is injurious to protoplasm, and its presence may make a particular habitat unfit for life. On the other hand, the fact that carbon dioxide is necessary for photosynthesis makes it a continual necessity for green plants. Fulton (1922) claims that chlorophyll is present in, or is the source of, pigment in protozoans, sponges, actinians, flatworms, and echinoderms. He thinks that hemoglobin is probably derived

from chlorophyll—phylogenetically and physiologically. A stagnant swamp that is saturated with carbon dioxide may be oxygenated by the photosynthetic activity of its green plants during the day but be uninhabitable for many animals at night. Aquatic plants serve three important functions: (1) the aeration of water; (2) the covering of the bottom; and (3) through disintegration, the enrichment of the water, thus making possible the growth of a greater volume of plankton. Plants have another important relation to animals in their ability to synthesize simple organic nitrogenous compounds that are essential for protein metabolism. Animals are not able to carry on nitrification or nitrogen fixation.

Plants not only furnish food for animals but serve them in many other ways, giving protection from radiant energy, changes in temperature and enemies, as well as favorable situations for the building of homes and the rearing of offspring. In any region the number of animals is roughly related to the amount of vegetation. Many animals have very specialized relations with particular plants. Some caterpillars will eat the leaves of only one genus, or even one species, of plant; some bees visit only one kind of flower. On the other hand, certain plants support from 200–500 species of insects. The caterpillar of the gypsy moth and the migratory locust will feed on almost any plant. The benefits derived from associations between plants and animals often accrue to the former as well as the latter. Plants are pollinated, defended, and distributed by animals. There are a few plants that capture and devour animals, and many microscopic species that cause diseases.

PLANTS AS FOOD FOR ANIMALS

Relations of Vegetarians to Plants.—Vestal (1914) in his excellent paper on the internal relations of terrestrial associations says:

> The majority of plant-feeders are adapted to eat herbage of nearly any kind: they are not restricted to particular species or particular parts of plants. They are non-selective feeders.

Most of them are only moderately specialized.

> Selective feeders belong with the highly specialized animals. . . . Highly specialized forms are thus enabled to avail themselves of oppor-

tunities denied to animals of generalized type; but while they avoid competition by the adoption of special kinds of food, or by a special habit of some other kind, they lack the versatility of the less specialized animals, being unable to adjust themselves to changed conditions.

They may be abundant at times but never become dominant through large ecological divisions. When a species becomes abundant, it is usually attacked by many predaceous species that have some flexibility in their food habits. "Animals with non-specialized habits, by taking whatever food is easiest of access, act as regulators." They are important in preserving the balance in nature. Baker, Korstian, and Fetherolf (1921) have given an illustration of man's effect on such a balance in the Wasatch Mountains. In that region the coyote is gradually being exterminated, and this leads to an unusual increase in its common prey, the snowshoe rabbit. In winter the rabbit feeds on the tender buds and twigs and has thus changed the aspect of the country by holding back the upward growth of many conifers for years. Dwarf vegetation is now quite characteristic. Forbes (1880) has discussed a number of similar relations between plants and insects. Autotrophic plants are of course dependent on light. In aquatic habitats they are therefore not found at great depths. Thermal stratification also limits the availability of carbon dioxide, phosphates, and nitrates. Such nutritive substances accumulate in deep water and are often deficient in strata near the surface at certain seasons (Atkins 1926). Both plants and animals tend to show more or less arrangement in zones above and below the shore lines of bodies of water (Abbayes 1932).

Miners and Borers.—Many insects in both aquatic (Natanson-Grodzinska 1932) and terrestrial (Stary 1931) habitats live within the leaves or green stems of plants. Such miners live within their living plant food. Borers in wood live largely on stored carbohydrates, on fungi or other organisms that grow in rotting wood, or on cellulose (Savely 1939). A few depend on commensal organisms, such as Protozoa or bacteria, which are able to digest cellulose.

Defenses of Plants against Animal Vegetarians.—Plants that are fed upon by animals often have adaptations that keep many animals from using them as food. Among peculiarities that are more or less effective for such purposes are thorns, saws, urticating hairs, hard or gritty exteriors, irritating crystals, ethereal

oils, bitter juices, alkaloids, etc. A plant that possesses any one of these is not necessarily adapted to ward off all vegetarians. Some expedients are effective against one feeder, and some against others. A donkey or goat readily browses on spiny plants; certain insects favor the milkweeds (which contain sticky, bitter juices) above all other foods. It cannot be said that any "adaptation" is effective under all circumstances. However, those that make plants avoided by animals are most prevalent where there is a dearth of plants for food, *i.e.*, in the desert.

Food Stores.—Animals that depend on vegetation for food often lay up stores to be used during seasons when little or no food is available. As stores have been discussed rather extensively in connection with other topics (pp. 118, 119), they will be touched on very little here. Beavers transport green branches to the bottoms of ponds and feed upon them during the winter. The California woodpecker makes holes in tree trunks to receive acorns. Many rodents store small seeds, nuts, grasses, or other vegetation in holes for use in cold or dry seasons. Perhaps the most interesting among provident animals are the harvesting ants, which hoard seeds in underground chambers. Wheeler (1910), in speaking of the work of Moggridge, says:

> In confirmation of Pliny and Plutarch he maintains that the ants bite off the radicle to prevent the seeds from germinating, a process which is also arrested by bringing them when damp with rain to the surface, spreading them in the sun and then carrying them back to the granaries. Some of the seeds sprout, nevertheless, either in the nests or on the kitchen middens.

On the other hand, the germination of certain seeds before they are eaten is said to obviate the necessity of cracking their coats by ants. Some species of harvester ants chew up seeds into a dough, which is molded into pellets and dried in the sun and, like the bread of man, may be invaded by fungi which multiply and make the mass more digestible (Wheeler 1911). According to Heim (1898), a Mediterranean harvester ant lays up stores in underground mud cells that are originally made by a beetle.

Crops.—A step beyond the storing of food is the raising of crops and the keeping of flocks. Outside the human race agriculture is practiced by ants, termites, and beetles. Certain ants feed on secretions, which are derived from animals but consist

largely of carbohydrates that come indirectly from plants. Ants feed thus from other ants, aphids, beetles, insect larvae, and scale insects. These sources of food are tended carefully, some being carried underground, inclosed in manufactured shelters, or placed in favorable situations on plants.

Types of Crops.—In regard to crops there are some variations among different agricultural insects, though probably no insect raises anything but fungi. The ambrosia beetles feed on fungus that grows on sawdust and other materials that accumulate in their galleries in deadwood. Termites use feces, sawdust, and other materials for culture media. The hairy ants in Africa make gardens from sawdust, feces from insect larvae and other organic materials, and raise several species of fungi. Leaf-cutter ants make beds from bits of leaves. The fungi that they cultivate are not found outside their nests and are pruned in order to produce peculiar growths, which are the only parts devoured. A female leaf cutter when ready to found a new colony carries away a "brick" containing fungus from her parents' nest and plants this on the first little bed of leaves that she makes, thus starting a new line of cultures. The leaf cutters have had a marked influence on South American vegetation. The rose, orange, coffee, chickory, mango, cabbage, and some other plants cannot be grown successfully as crops where these ants are abundant, but some plants (eucalyptus, ramie, grasses, bay, magnolia, cucurbits, etc.) are not molested by the insects. Among certain termites in Ceylon only the queen and larvae eat fungus, the workers and soldiers subsisting on other foods (Doflein 1906).

Origin of Agricultural Habits.—Wheeler (1907) states his belief that all ants were originally exclusively entomophagous. Only a few species have become storers or agriculturalists. Attiid ants, certain termites, and ambrosia beetles raise practically pure cultures of various fungi. According to Wheeler, Von Ihering first suggested that such habits arose from eating fungi that developed on stored foods. Wheeler says in regard to the leaf cutters:

These insects in the fierce struggle for existence, everywhere apparent in the tropics, have developed a complex of instinctive activities which enables them to draw upon an ever-present inexhaustible food supply through utilizing the foliage of plants as a substratum for the culture of edible fungi. No wonder, therefore, that, having emancipated them-

selves from the precarious diet of other ants, which subsist on insects, the sweet exudations of plants and the excrement of phytophthorous Rhynchota, the Attii have become the dominant invertebrates of tropical America.

GALLS

Character of Galls.—Galls are abnormal growths produced by mechanical irritation or the presence of chemical substances. Though a few occur on animals (crab galls on corals, glochidial galls on fishes, growths about trichinae and chigoes, etc.), they are particularly characteristic of plants and usually furnish food and shelter for plants or animals that live within them. They may be produced on plants by the presence of bacteria, slime molds, fungi, rotifers, copepods, nematodes, mites, or insects. Plant galls are divided into two groups: (1) kataplasms, which consist largely of undifferentiated parenchymatous tissue; and (2) prosoplasms, which contain a variety of tissues. Kataplasms are in a sense deformities of parts that are already present, and prosoplasms are to a greater extent new growths that are peculiar and highly specific for each species of maker. The former type are produced by parasitic plants, slime molds, rotifers, copepods, nematodes, Orthoptera, Neuroptera, Coleoptera, Lepidoptera, muscid flies, chalcids, and sawflies; the latter are probably caused only by arthropods (Cook 1923) and have definite sizes, tissue forms, and times of development (Wells 1934). Both kataplasmic and prosoplasmic galls are produced by flies (*Itonididae*, *Trypetidae*), Hymenoptera (*Cynipidae, Tenthredinidae*), bugs (*Aphididae, Psyllidae*), beetles, lepidopters, and mites.

Stimuli Causing Galls.—There has been much discussion concerning the specific stimuli that cause galls to develop. There have been advocates of mechanical stimulation as the sole cause of galls, and those who contended that galls were entirely due to the presence of chemicals. Most of the evidence seems to support the latter view. It was formerly supposed that insect galls were caused by a substance that the female injected or the injury that she inflicted when she deposited her eggs, but very few instances are known that are explainable on such a basis. Though there are some exceptions, insect galls usually do not begin to develop until their larvae hatch from the

egg and become active. In many cases the greatest proliferation of tissues may not take place near the larva but at some distance from it. This indicates that the abnormal growth is due to a chemical substance that stimulates cell proliferation. The larva continually obtains nourishment through its mouth from the tissues surrounding it. Folsom (1923) says:

> The larva by accelerating the rate of change from starch to sugar renders available to the plant more food than usual and therefore stimulates the activity of the protoplasm toward greater cell-growth and more rapid cell-reproduction. Thus the gall as well as the larva draws food from the nutritive zone.

Plant physiologists generally make more cautious statements and await further evidence. Since the days of Malpighi (*De Gallis*, 1686) there has been speculation as to the stimuli causing galls. "The preponderance of opinion among recent students is that some form of organic substance or substances is given off from wounded cells, egg surface, or from some part or all of the larvae" (Wells 1934). In certain Australian galls there are specific differences between growths produced by male and female insects of the same species.

Host Relations of Gall-producing Animals.—Gall-producing animals usually show a considerable degree of specificity in the plant hosts that they attack, and some types of plants support great numbers of galls. Felt (1911) listed 1,400 species of galls in North America. Galls may occur on any part of a plant (root, stem, bud, leaf, leaf vein, flower, seed, etc.), but the situation and the form of the galls caused by each species are usually quite characteristic. Insects and other animals that do not produce galls may live in them. Folsom (1923) mentions an instance where 30 species of insects were reared from one kind of gall. Heindel (1905) found 32 species of insects in the willow-cone gall: 1 gall maker, 10 inquilines, 16 parasites and hyperparasites, and 5 transient or accidental guests. The oak, hickory, and grape support many gall producers. Felt (1910) states that the genus Caryomyia is restricted to hickory food galls and that Cincticornia is probably confined to oaks. He also lists 18 species that are found on asters, 35 on golden rods, and 46 on willows.

THE RELATIONS OF ANIMALS TO FLOWERS

The relations between flowers and insects furnish some of the most remarkable instances of adaptation in the whole of nature and have been much discussed by naturalists. Robertson (1899) believes that flowers were first visited for nectar, and such adaptations as the sticky pollen and convenient landing places were developed later to insure the calls of insect visitors. At present insects and other animals receive notice of the presence of flowers by particular colors and odors. They feed upon nectar, pollen,



FIG. 112.—Bee visiting a salvia flower. It alights on a petal which serves as a landing platform. The stigma of the flower rubs along the back of the bee and thus scrapes off pollen.

and other substances that the flowers furnish and in return benefit the flowers by carrying pollen. Bouvier (1905) says:

To summarize: (1) Nectar and the nectaries are certainly intended primarily for the plant itself and do not prove the adaptation of the flower to the insect. (2) The colors and perfumes of flowers may be perhaps the result of such adaptation, but in any case they strongly attract anthophilian insects, signaling to them the presence of booty. (3) In many cases, if not all, the complicated forms of the flowers must be attributed to the adaptation of flowers to their insect visitors. . . . It is almost unanimously conceded nowadays that the Mellifera, at least insofar as their collecting apparatus is concerned, are beautifully adapted to the flowers, but, despite the fact that practice has shown that plants are in every way more plastic than animals, it is still strangely disputed that flowering plants have adapted themselves to bees. If there does exist any reciprocal modification between the Mellifera and flowering plants, it is not at all necessary to suppose that one group has been modified for the benefit of the other. Each has evolved on its own account. Explained thus, the many objections to reciprocal adaptation are overthrown. The bee has but one object, the pursuit of food, and all

things which aid him in it are welcome. Usually the plant profits thereby; sometimes it suffers. On the other hand, the plant seeks only to assure its propagation and all its modifications tend only toward that goal. It is only indirectly that colors and perfumes are of advantage to insects; the complicated flower, most favorable to the reproduction of the plant, is to the bees an obstacle. . . . It is by no means for the benefit of the plant that the collecting apparatus of the bees is modified, but only that the bee may better nourish itself. On the other hand, it is to the distinct advantage of the plant and its propagation that flowers are modified in shape, color and odor. The insect has gained by the conformation of the flowers; the flower by the visits of the insect.

Pollination by Animals.—The great benefit that certain plants appear to receive from the visits of insects and other flying animals to their flowers is cross-pollination. Plants, as a whole, may have various means within themselves that help to accomplish this (unisexual flowers, a difference in the time of maturation of the pistils and stamens, differences in the lengths of stamens and pistils, traps for insects, etc.), but some are absolutely dependent upon the visits of particular insects and are adapted to them by possessing certain foods, odors, colors, patterns, and forms. The adaptations of flowers may also be such as to prevent the visits of guests other than the usual pollinators. There are also many adaptations for loading visitors with pollen (dusters, slappers, exploders, pumps, etc.), and elaborate mechanisms for receiving pollen.

Visits to Flowers for Food.—Certain insects, birds, and other animals are specially fitted for feeding on nectar, pollen, and other flower products, and many can subsist on nothing else. Many moths that do not frequent flowers are poor flyers and have degenerate tongues (Ord 1900). Many orchids with deep corollas are pollinated by moths with long tongues. Pendulous flowers are accessible to few insects but bees. Many bees feed largely on pollen and have special adaptations for collecting and transporting it. Moths, flies, and birds, as a rule, make little use of pollen and usually have less specialized means for carrying it, if they do so at all. Flower visitors may be classified as *polytropic,* visiting many species of flowers; *oligotropic,* visiting few species; *monotropic,* visiting only one species. Oligotropic bees are usually solitary and have a short flying season when their special flowers are in bloom. By visiting few kinds of flowers,

they more or less avoid competition. A honeybee is essentially oligotropic, for it usually feeds largely from one species of flower at a time. Insects, especially bees, often have restricted feeding habits for both pollen and nectar (Graenicher 1935, Robertson 1925). A bee may collect pollen from one type of flower and nectar from another. Apple blossoms are pollinated mostly by bees of the genera Andrena and Halictus, not by honeybees (Apis), and by syrphid flies (Atwood 1933, Phillips 1933).

Time of Blooming Related to Pollinators.—In general, the time of blooming of entomophilous flowers coincides more or less with the time, both as to day and season, when their pollinators are flying. Robertson (1895) pointed out that introduced species generally have a longer blooming season than native plants, he believes, because they are subject to less competition. Aquatic plants also bloom longer than comparable terrestrial species, probably for the same reason. In a general paper Robertson (1924) discusses the times of blooming of various Illinois plants in detail. Plants that mostly bloom before July include: (1) low plants, which are shaded by trees or other taller vegetation; (2) 90 per cent of the trees and 64 per cent of woody climbers, though many do not begin to bloom before June; (3) 53 per cent of the shrubs; (4) 68 per cent of all woody plants. Fifty-two per cent of woodland herbs begin to bloom in March and April. Social flowers make up 60.4 per cent of plants in bloom in October; nonsocial flowers compose 75.7 per cent of those in bloom in April. White flowers are dominant in early spring and late fall; yellow and red, during the warmer months. The season for maximum blooming for annual and biennial plants is a month later than that for perennials. Taller herbs bloom later than shorter plants do. Annuals compete with each other in their blooming season less than perennials. Anemophilous flowers are most common in spring, before there are many insects. The short-tongued bees, in general, visit the more primitive flowers, and those that frequent the social flowers are obliged to share them with flies and primitive hymenopterans. Flowers that are adapted to receive visits from a variety of insects often show a tendency to be social and bloom late.

The succession of blossoms throughout 24-hour periods is well described by Kerner and Oliver (1895), who give "floral clocks" for various localities. Insects by flying at a particular

time of day find their food flowers open and thus are not associated with species that fly at other times in order to obtain food from other flowers. Winn (1902) was surprised to find milkweed blossoms invaded by a host of moths just after the sunlight had faded away in the evening.

Adjustments of Flowers to Visitors.—Flowers not only furnish nectar and pollen for food but are visited by animals for various other purposes. They serve as sleeping places and refuges. Crab spiders, mantids, and assassin bugs lurk in flowers and capture little insects that come for food. Many of the animals that visit flowers are of no benefit, and many are injurious. Needham (1900) noted that *Iris versicolor* was pollinated by bees, flies, and beetles but robbed by butterflies and weevils and eaten by orthopterans, moths, and flies. Many flowers are protected from creeping marauders by honey exposed below the flowers, isolation by water, sticky secretions, spines, slippery surfaces, wax, etc. Protection devices against undesirable flyers are chiefly in the flower itself. Lowe (1921) noted that in a wet season bumblebees, instead of taking nectar in the usual way from the flowers of the scarlet runner bean, bit through the side of the floral tube and thus robbed the flowers without coming in contact with the anthers. The wounds permitted the short-tongued honeybees to join in the robbery. The next season was drier, and the flowers of the scarlet runner were apparently too tough for the bumblebees to bite through. They fed by inserting their tongues in the usual way, and honeybees did not visit the flowers. When conditions are favorable, a particular kind of flower may have a very large number of species of visitors. Kellogg (1905) reports the following numbers for four plants: *Pastinaca sativa*, 275; *Sium cucutaefolium*, 191; *Cicuta maculata*, 238; and *Solidago canadensis*, 146. Robertson (1922) observed 143 species on sunflowers in Illinois. Weiss (1923*a*) on *Pastinaca sativa* reports during 26 days: 173 Hymenoptera, 14 Coleoptera, 9 Lepidoptera, 6 Hemiptera, 1 Neuroptera; and on *Asclepias verticillata:* 52 Hymenoptera, 42 Diptera, 16 Lepidoptera, and 3 Coleoptera. Above the timber line, Kenoyer (1917) found that flowers that required pollination were mostly bee flowers.

> It seems that the flowers above timberline are as much visited by insects as those of lower altitudes, and I have no reason to suppose that they are any less dependent for pollination upon their insect visitors.

Kenoyer observed no honeybees, but bumblebees were common. The more specialized the flower the fewer will be the species that visit it.

Odors and Colors as Agents Advertising Flowers.—There has been much discussion concerning the relative potency of colors and odors in giving notice to pollinators of the presence of flowers. Lutz (1924) has properly pointed out that many of the experiments intended to test color discrimination have been performed in an uncritical way, without adequate knowledge of what the physical character of the "colors" used represented and of what stimulating agents were received by the animals under experiment. Von Frisch (1920, 1923) maintains that color is more important for bees in finding food than odor. His tests indicate that bees perceive about the same range of odor sensations as man. He has shown that bees on returning to a hive notify their mates of the presence of food largely through odor stimuli and that in this connection sounds are of little or no importance. Lutz (1924) and Von Frisch (1923*a*) discovered that bees perceive ultraviolet flowers in addition to those having colors observed by the human eye. Lutz believes that the so-called bright colors of plants are due to physiological processes, which result from "by-products of plant metabolism" and that they are little concerned with the recognition of flowers.

Colors of Flowers.—Green flowers, as a rule, are not entomophilous and often are self-fertilizing; the few insects that visit them belong to the less specialized families. Colors in flowers are often those that appear to make good contrasts with green foliage. Flowers appear, in general, to be larger and brighter where insects are rarer, as in alpine meadows. Sometimes in flower clusters there are sterile, bright-colored, "attracting" flowers at the top and comparatively inconspicuous, food-laden flowers below. Knuth (1898) cited extensive evidence that flies see flowers and visit them through visual stimuli. Clements and Long (1923) have shown that if the corollas are removed from flowers, the visits of insects decrease in number. The exposure of nectar increases such visits. Artificial flowers received only one-eighth as many visits as the natural blossoms that they simulated; painted flowers received only half as many. Flowers placed under glass to prevent the escape of odors were visited. Clements and Long conclude that, for the honeybee, color and form are four times as potent as odors in indicating the presence of

flowers. Flowers pollinated by birds are generally red or orange in color, hold much honey of low concentration, and have lips and odors. Their corollas often have protecting reinforcements against hard beaks (Pijl 1934, 1936, Spennemann 1932, Van Leeuwen 1930, 1933, 1933*a*). Many of them project above surrounding leaves. Flowers pollinated by bats are usually large, strong, wide, bright or dull colored, contain much mucilaginous honey and pollen, are night-blooming, and are easily accessible. Bats that feed from flowers have pointed snouts and long slender tongues (Pijl 1934, 1935). Some flowers attract male insects because they resemble females of the same species (Faegri 1933). Bees commonly establish temporary associations with productive flowers of certain colors and consistently visit them (Kugler 1931, 1933).

Odors of Flowers.—Kerner and Oliver (1895) classify flower odors as idoloid, aminoid, and benzoloid. Certain flowers that are carrion scented are visited by flesh flies and carrion beetles. Night-blooming flowers are often white and strong scented. Ord (1900) believes that night-flying moths generally avoid light-colored flowers and that white is more of an impediment than a help to flowers that depend on moths for pollination. He believes that odor is the potent factor. Lutz (1924) also stresses the importance of odors in giving notice of flowers to insects. He observed that many insects that went against the wind found flowers directly, whereas those that flew with the wind often passed them. As has been mentioned, bird-pollinated flowers are generally odorless; but those visited by bats are nocturnal and "unpleasantly musty or sourish in scent" (Pijl 1934, 1935, 1936). Some birds peck holes through the sides of corollas to obtain honey. Certain flowers (Stapelia, etc.) have odors that resemble that of decaying meat. These are visited and pollinated by various flesh flies (Calliphora, Lucilia, Sarcophaga). These flies even deposit larvae, though no suitable food is available for them, and they die (Martelli 1932).

Relations of Colors and Odors of Flowers.—Lovell (1914) pointed out that color and odor in flowers may be to a certain extent mutually exclusive. A flower that emphasizes one is often lacking or weak in the other. Insects visit flowers for food and use any means that they can to find and secure it. The absence of both color and odor does not cause a flower to be

wholly neglected if it contains nectar or pollen. Diptera are attracted by a wide variety of fruity odors, some of which are characteristic of flowers. Bees feed on overripe or even decayed fruit, glandular secretions from the vegetative organs of plants, and secretions from aphids and from greenish flowers. These facts do not prove, however, that conspicuousness is not an advantage to a flower. Any surface, bright or dull, will be visited if bees find that it contains food, but it will not be discovered so readily if it is dull. Lovell says:

> Insects perceive the colors and forms of neglected flowers, and the rarity of their visits is the result of their memory of the absence of food materials, not because the flowers lack an agreeable odor, which is often not the fact. Colors and odors attract the attention of insects, but bees in their visits to flowers, previously examined by them, are guided largely by memory of past experiences; they are able to associate different sense impressions and unconsciously make analogous inferences.

Lovell is undoubtedly right in these statements, but the whole question should be gone over experimentally with more carefully analyzed and better known "color" and "odor" stimuli. Bees can discriminate and form associations with particular patterns (Turner 1911).

Types of Pollinators.—The most important pollinators of flowers are Hymenoptera, Diptera, and Lepidoptera, but beetles, birds, and even such animals as snails and bats may serve as pollinating agents. Among insects the most specialized types are those which have built up the most intimate associations with flowers. The primitive Hymenoptera prefer exposed nectar; flies and Lepidoptera are not important pollinators for many flowers from which they suck nectar (Robertson 1923*a*). Bees get all their food from flowers and are not in the same "ecological class" with other hymenopterous insects. Robertson (1922) among 437 species of entomophilous flowers found bees in 95.4; flies in 60.4; and Hymenoptera other than bees in 43 per cent. Counting the number of visits, bees represented 33.3–60.6 per cent; and other hymenopterans, 1.6–16.9. Polytropic bees may visit flowers of various colors, forms, and odors; oligotropic bees may depend on one family or species to which they are strikingly adapted. Flowers pollinated by birds are usually red in color and have deep corollas. They probably represent

flowers that at one time were served by lepidopters and have been more or less taken over by birds. The red clover in New Zealand was sterile until bumblebees were introduced (Schimper 1903). In northern forests, trees are generally anemophilous; in tropical forests, entomophilous (Warming 1909). The geographic distribution of certain plants and insects is identical. Riley (1892) states that each species of yucca has its special species of Pronuba moth that is associated with it, and he described one species in detail that has long served as a classical example of interdependence between insect and flower. In this case the adult moth does not get any food from the flowers of the yucca. It hatches in one flower, from which it takes a supply of pollen, then flies to another flower, lays its eggs in the ovary, and plasters about the pollen it brought over the stigma. Insect-pollinated flowers are usually monoclinous, and their pollen is often moist, sticky, or adhesive. Many flowers, particularly certain of those with deep corollas that are invaded by hard tongues or beaks like those of moths or birds, have mechanisms for attaching pollinia which are shed in another flower. Milkweed pollinia become attached to the claws or hairs of insects, and these are removed by a mechanism in the next flower visited. Many specialized flowers are so constructed that only one type or species of insect can enter. Schimper (1903) says:

> Numerous flowers are robbed and pollinated by the most varied visitors, as their pollen and nectar are offered freely to all, or are easily accessible. Other flowers are, in greater or less degree, adapted to certain definite visitors either because their allurements presuppose certain characteristic tastes, or the access to their nectar is only possible to visitors possessed of certain bodily shape or certain faculties.

PLANTS AS SHELTERS FOR ANIMALS

Many animals use plants as refuges and are thus protected from enemies, evaporation, extremes of temperature, and other unfavorable environmental conditions. Certain katydids and spiders commonly rest in flowers or seed pods. As has been mentioned (p. 412), bromeliads support a large number of animals that are in many cases flattened or otherwise adapted to live in the spaces between the leaves. The leaf rollers and webworms commonly fasten leaves together to make nests. The ants of the genus Oecophylla cooperate in holding large leaves together

and, being unable to spin, use their larvae as living shuttles so that the threads produced bind the leaves into a pear-shaped nest. Many other insects, spiders, myriapods, snails, amphibians, reptiles, birds, and mammals commonly nest in trees or smaller vegetation. Prairie birds commonly dig little hollows for their nests and take advantage of little clumps of plants for shelter from winds (Du Bois 1935). Not only does an area of vegetation furnish shelter from desiccation and equalize temperatures, but leaves exert a selective action on light absorption so that beneath them there are fewer actinic rays (Daxer 1934).

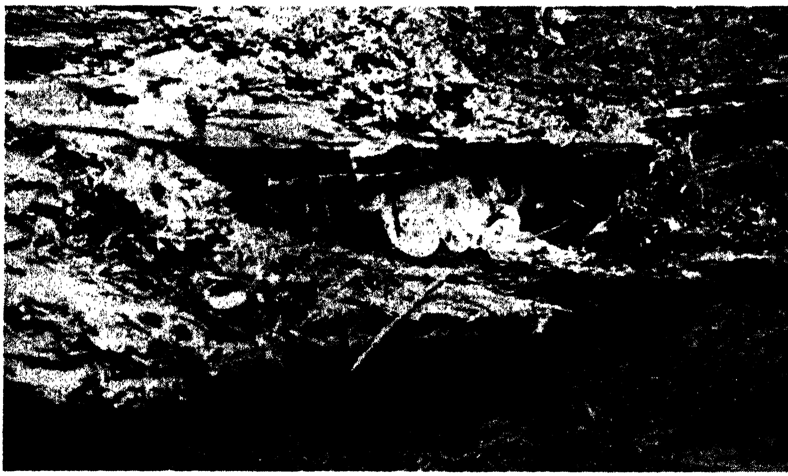


FIG. 113.—A centipede with its brood of young in a cavity in a rotten log.

Tree frogs commonly use insect-catching pitcher plants as hiding places during the day (Andrews 1928). In Alabama the writer once looked into 100 of these plants and found two of them thus occupied. The larva of a moth not only invades and feeds upon the pitcher plant but passes the winter in a carefully constructed hibernaculum in its base. This caterpillar cuts a groove around the inside of the leaf that it inhabits; the top of the leaf then droops over and closes the opening; thus the invader is protected from parasites (Jones 1907). Mosquito larvae are protected from predaceous enemies when they live among thick mats of vegetation; even Gambusia does not attack them. Eidmann (1935) described an interesting community of animals inhabiting poplar trees. Borers had produced galls; these had

been opened by woodpeckers which devoured larvae and pupae. The cavities left had then been occupied by a crabromid. Dead trees and logs are commonly used as shelters for breeding or hibernation by small animals (Fig. 113).

SEED DISPERSAL BY ANIMALS

The seeds of many plants are absolutely dependent on animals for dispersion and others are often transported on animals by accident. Everyone is familiar with the ticks, burrs, and similar fruits that grow along the paths of men and other animals. Kerner and Oliver (1895) state that 10 per cent of the flowering plants have seeds that are distributed by clawed or barbed processes—some by creeping along the ground, others by attachment to animals. Some seeds adhere to animals by means of sticky secretions on hairs or stalked glands. They may take long journeys with their living carriers and are often plucked off and deposited on fertile soil. Forbes (1885) describes the Pisonia tree of the South Seas as having spiny glutinous seeds which are carried to remote oceanic islands by herons and sea birds. The small seeds of many aquatic plants are carried in the mud that adheres to animals that come to shores to drink.

Fruits Eaten by Animals.—Ripe fruits, when luscious, showy, and odorous, attract the attention of animals and may be carried about. Unripe fruits are often protected by being hard, bitter, and covered over by foliage. In some cases they are even poisonous. The seeds of pine and nut trees are commonly planted by squirrels and other animals. Though many are eaten and destroyed, a considerable number are thus placed in favorable conditions for germination. The gooseberry has four means of dissemination: wind, gravity, running water, and animals. Seeds are distributed over long distances largely by water, winds, or animals (Cooper 1922). Robertson (1897) describes certain seeds that have crests that protrude from their coats. He asserts that such appendages serve as "handles" for the mandibles of ants and that certain of the seeds have no means of dispersal except by ants. Some seeds that are adapted to such dispersal have an edible portion on the outside and are discarded after this is eaten.

Many fruits commonly eaten by animals contain seeds that have hard coats, contain bitter substances, or have other qualities that make them inedible, but other fruits bear seeds that

can pass through the alimentary tracts of animals without injury and are deposited with fertilizing materials in the feces. Kerner and Oliver (1895) carried on extensive experiments concerning the viability of seeds eaten by birds and also found that a few seeds might occasionally pass through mammals without losing their viability. A few millet seeds grew after passing through a cow, and lentils survived journeys through the horse and pig, but most seeds were crushed in the mouths of such animals. Birds fall into the three groups: (1) those that grind up the hardest seeds (pigeon, crossbill, goldfinch, etc.); (2) those that destroy soft seeds but allow hard seeds (cherry seed) to pass through (raven, jackdaw); and (3) those that deposit many viable seeds that have passed partly or wholly through the alimentary canal. The blackbird, thrush, and robin cast up from their crops all stony fruit seeds more than 3 mm. in diameter but small seeds (75 per cent viable) pass out with their feces. Some seeds passed through such birds in three-fourths of an hour. Recent work has shown that barberry seeds are commonly viable after passing through animals. The protective coats of seeds are, in general, adapted to the types of gizzards that birds carrying them possess (Zazhurilo 1931). Several kinds of seeds are commonly carried on the bodies and wings of birds (Steenis 1932, 1934). The dung of animals in Africa was found by Burtt (1929) to contain many living seeds.

CERTAIN SYMBIOTIC RELATIONS BETWEEN PLANTS AND ANIMALS

Aside from symbiotic relations between animals and plants in connection with flower pollination and seed dispersal, certain intimate relations deserve to be mentioned. There are many algae that grow on the shells of snails (Iltis 1913) and are carried about. They probably derive some benefit from such association. The snails may use portions of their own gardens for food and are camouflaged by them to some extent. Fulton (1921) reviews the few cases where algae live in actinians and flatworms. He concludes that such plants are slaves and merely serve to nourish the animals in which they live without receiving much benefit in return. If such animals are kept in the dark, they feed on their contained algae, which finally disappear. Buchner (1921) believes, however, that many plants live in symbiotic

relations within animal cells. He describes various algae and bacteria that dwell in protozoans, actinians, ctenophores, turbellarians, annelids, rotifers, bryozoans, echinoderms, molluscs, tunicates, and insects. He also agrees with Brues and Glaser (1921) that certain fungi that live in insects are symbiotic. Particular groups of enlarged cells (mycetostomes) harbor the fungi in the fat bodies of Coleoptera, Hymenoptera, Lepidoptera,



FIG. 114.—An acacia with large stipular thorns which serve as homes for stinging ants, Colombia.

Diptera, Hemiptera, Orthoptera, and Corrodentia. Various methods are employed to transfer the fungi from parent to offspring. In certain beetles, pyrosomas, cephalopods, and fishes symbiotic plants are luminescent.

Ant Plants.—Among the most interesting of the symbiotic relations between plants and animals are those of the ant plants. Most of these plants provide shelter and food for their guests, which by their presence defend the plants from browsing animals and phytophagous insects. In America the ant plants are largely acacias and cecropias (Safford 1923). The former usually have hollow stipular thorns which may serve as ant dwellings and glandular secretions near the tips of the leaves which

furnish food. Acacia ants drive away leaf cutters (Folsom 1923). The cecropias are provided with many small chambers in their stems, and food is present on their petioles, but many of their ants feed on the secretions of aphids which are kept inside the stems. The ant plants of the Malayan region have been carefully described by R. W. C. Shelford (1916). The common types have numerous spongelike, intercommunicating spaces in a succulent tuber and many small openings to the exterior. Schimper (1903) does not believe that these plants developed in association with ants. He looks upon the spaces as respiratory adaptations which have been secondarily used as a dwelling by the ants. Schimper describes many types of ant plants, including some that provide dwellings in leaves and outgrowths from stipules. Wheeler studied an ant plant in British Guiana that had 50 species of organisms associated with it: 20 ants, beetles, coccids, etc. (Cockerell 1922). Heim (1898) describes groups of ants that live in and defend the tender buds of palms. After describing such more or less accidental, but nevertheless fortunate, associations, Heim discusses various degrees of adaptation in plants and ants which permit symbiotic relations with each other. Ridley (1910) points out that ants associated with plants may be beneficial, neutral, or injurious.

PLANT ENEMIES OF ANIMALS

There are a number of types of plants that do injury to animals. The spiny seeds of the Pisonia tree often, by becoming entangled in the wings and feathers, cause the death of birds that normally function in their distribution (Forbes 1885). Animals that are chased or fall among saw-edged or spiny plants may be killed.

Plants That Catch Insects.—The most important of the plant enemies of animals are the insect catchers. These are often found where available nitrogen is deficient and animal diet serves to supply this necessary food element. The sundew, Venus'-flytrap, and pitcher plant have quite specialized means for capturing insects. The bladderwort entraps crustaceans and other small aquatic animals. It has been admirably described by Needham and J. G. Lloyd (1916) and F. E. Lloyd (1933). Schwartz (1905) and Lochhead (1918) have given good general accounts of insect-catching and insect-eating plants.

Some insects take advantage of the pitcher plant, and what is a dangerous trap for other species becomes for them an especially safe refuge. A mosquito larva habitually lives in the water that stands in this plant (Mitchell 1905). Hubbard (1896) discusses certain moths that make their homes in pitcher plants and crawl about readily on the spiny inner walls. Their larvae allow the liquid in the pitcher to escape by cutting a hole near the base, which insures a dry interior. A wasp also uses pitchers as a place to rear her young, stuffing in grass and plant fibers which float above the liquid at the bottom. On this raft she constructs a few mud cells. A spider is accustomed to spread its webs across the mouths of pitchers and to spin its cocoons inside. The maggots of sarcophagid flies are commonly found at the bottoms of pitchers. They feed on the masses of entrapped animals and thus rob the plant. Jones (1904) extended Hubbard's observations on pitcher-plant insects somewhat and also described the capture of victims in detail.

Fungi That Attack Animals.—Certain bacteria and other fungi commonly attack animals. There is one group (Laboulbeneaceae) that infects by means of explosive fruits which shoot spores at passing insects. Cordiceps commonly sends its hyphae through the bodies of white grubs. There are a number of fungi that cause diseases in the skins of animals. These are quite common in dark races of men in the tropics. Bacteria are, of course, causes of disease in many types of animals.

ANIMALS THAT CARRY PLANT DISEASES

Among phytopathologists there has been steadily increasing interest in, and recognition of the importance of, animals as carriers and inoculators of the diseases of plants. Gardner (1918) states that plant diseases are usually spread by winds, waters, birds, insects, and some other animals. Man has been especially important as a carrier for long distances, through the marketing of his crops and shipment of propagative parts. Domestic animals spread soil-infesting parasites; birds are particularly important in the distribution of tree diseases.

Insects are the chief inoculators of plants with certain diseases. Lochhead (1918) states that flea beetles eat holes in the leaves of potatoes and permit blight to enter; aphids and other insects carry apple and pear blight; the squash bug, cucumber beetle,

flea beetle, melon aphis, and ladybird beetle carry cucurbit wilts. The activities of the plum curculio allow brown rot to enter. Tree crickets are said to carry canker and cane blight. Folsom (1923) says that fire blight is carried by bees and other insects to the nectaries of flowers, where it multiplies and from there invades a plant. Some insects are able to carry the organisms causing cucurbit wilt through the winter in their alimentary canals. Rots, cankers, and mosaic diseases may all be found connected more or less with insects.

CHAPTER XII

INTRASPECIFIC RELATIONS

The relations between animals of the same species are various, ranging from those associated with competition for territory or food to those connected with social life and polymorphism.

Competition.—Among animals the individuals of a single species most nearly occupy the same habitats and show the greatest degree of similarity in requirements for food, protection, and reproduction, even when they are compared with closely related species or groups. Accordingly, competition is most keen among individuals of the same species. More young barnacles settle on the rocks along the seashore than can come to maturity. All through nature there is adaptation to loss of individuals through intraspecific competition. Even within the bodies of mothers, certain ovarian eggs are sacrificed in order that others may survive or have the advantage of better conditions for development. It is the usual condition in nature to have more individuals produced than can possibly survive. Thus is provision made for loss through intraspecific and interspecific competition and from other causes. The survival of individuals in intraspecific competition is, in part, due to innate ability, but chance fluctuations in environment may operate in such a way as to favor maladapted or comparatively unfit individuals. Every individual struggles to survive—against unfavorable conditions in the environment, against other species of animals that seek to devour it or to keep it from existing for other reasons, but most of all against other individuals of its own kind.

Cooperation.—On the other hand, there is more or less of a tendency to cooperate all through the animal kingdom. It finds its inception in the essential adjustments between cell parts and between the cells of metazoans; it reaches its climax in the complex cooperative associations of colonial and social animals. Huxley (1912) has stressed the fact that the chief characteristic of individuality is independence, which is usually

associated with more or less toleration of fluctuations in environment and a certain consequent immunity to elimination through accidents. An individual that sacrifices independence in order to cooperate usually gains a greater degree of ability to survive and becomes a part of a larger social unit. A natural result of cooperation is division of labor, which results in tissues, organs, castes, and other parts of great wholes. Such parts are specialists for particular functions. In order better to preserve its race, an animal may give more or less care to its own reproductive products, which are in a sense an extension of its own individuality. Thus a more or less permanent society may be established and continue by an overlapping through two or more generations.

Alternation of Generations.—Another peculiar type of adjustment to various conditions in the environment has come about through the more or less regular alternation of different types of individuals through successive generations. During times when (or in situations where) conditions for propagation are favorable, new individuals are often produced rapidly and by simple methods; in environmental conditions that are less favorable, other types of individuals occur which propagate by methods that produce more resistant products, or products that are more likely to possess variations that may survive in the conditions that obtain.

Sex Relations and Reproduction.—The relations of individuals of a species in connection with reproduction often attain great complexity among dioecious types. There are often elaborate activities connected with mating. Among polymorphic species there may be a high degree of specialization of the sexes for various functions concerned directly or indirectly with reproduction. As so many of the important intraspecific relations of animals are concerned with reproduction, it seems proper to begin this chapter with a discussion of sex relations. After that, colonial and social life, polymorphism, and alternation of generations will be considered.

SEX RELATIONS

Sex Differences.—Among many species of animals the sexes are of approximately equal size, but among others there is often great discrepancy between the average size of males and females. Among certain species of worms, crustaceans, and rotifers,

the male is always minute. Some of these tiny males are parasites on their females, and some have no digestive system but receive enough nourishment from the egg to furnish energy for their short lives. A female seal is a timid creature, only a fifth as heavy as her pugnacious mate; a queen termite may weigh a thousand times as much as a king. Female spiders are usually larger and more pugnacious than males. As a rule, females are larger than males when they chiefly exercise their primary function of nourishing eggs and young; males are small when they devote their sexual activities to seeking out and fertilizing females or their eggs. McCook (1890) states, however, that among the



FIG. 115.—A male stag beetle, which is larger than its mate and has extravagantly developed horns on its head. Nigeria.

species of running spiders the size of males in relation to females increases in proportion to the amount of moving about that the adults do. In some species the males are larger than females, which is quite unusual among spiders. When there is competition for mates or when the individuals of one sex protect those of the other from danger, the sex that takes the aggressive role is commonly larger. There are many exceptions to such rules, however. The male dogfish, *Amia calva,* for example, makes a nest, cares for the eggs, watches over the young, and fights enemies but is smaller than the female. In many groups of animals there is a tendency for males to be small and inconspicuous or wholly absent for many generations (Causey 1935).

Numerical Ratio between Sexes.—The numbers of males and females are nearly equal in some species and quite different in

others. Among vertebrates males and females commonly occur in about equal numbers. Some phyllopod crustaceans are known only as females, and in other species males appear only at certain seasons or during particular years. Many cladocerans, rotifers, and aphids pass through a number of generations without males, reproduction taking place through the parthenogenetic development of eggs. In studying the rotifers in Danish ponds Wesenberg-Lund (1923) found that the life of males was often only a few hours in length and never more than four or five days. Periods of sexual reproduction were commonly preceded by an enormous increase in numbers, and before such periods males were rare or absent. Wheeler (1916) has described the nuptial flight of the bulldog ant in Australia and says:

> As soon as a male (and there were apparently hundreds of males to every female) captured a female on a bush, other males surrounded the couple till there was a struggling mass of ants forming a ball as big as one's fist.

On the other hand, Sherman (1914) after long observations of ruby-throated humming birds in Iowa concluded that there were six times as many females as males. Sex ratios are doubtless adapted to particular conditions of reproduction and of environment, but the exact nature of such adaptations has in most cases not been determined. In some species of animals (honeybee) males have been reduced in numbers, but other species (seal) appear to be maladapted in that there is a great number of nonfunctioning and apparently unnecessary males (Parker 1915). More females may be present among certain species because representatives of that sex have greater vitality and tend to live longer than males (Geiser 1923). This Geiser (1924) believes to be associated with the presence of two x chromosomes in females. Among some animals there is a variation of sex ratios at different seasons.

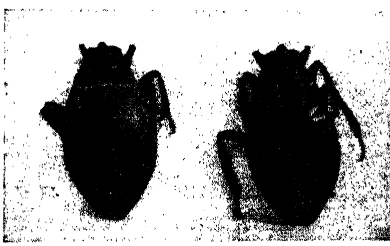


FIG. 116.—Water bugs; female and male are about the same size. The latter carries eggs, stuck on his back by his mate, until they hatch. Colombia.

Sex-determination and Environment.—Environment often plays a role in the determination of sex. Animals differ in the

degree of control that may be exercised by factors outside their bodies. In rotifers and bees, males are apparently produced by the parthenogenetic development of eggs which will develop into females if fertilized. There is also the possibility in such cases that two types of eggs are present, one of which must be fertilized and the other not. In aphids and cladocerans both males and females may be produced from parthenogenetic eggs. Sumner (1922) gives instances where sex is determined in the sperm or egg or by external factors. In some instances of apparent control of sex by variation in environmental factors, there has been only a greater mortality of germ cells that would have produced males or females. Geiser (1923) believes that in such cases females are more likely to survive. In many species of animals sex is apparently determined by the combination of Mendelian characters and is, therefore, determined before a particular individual begins its embryological development. Many investigators believe that the metabolic states of the eggs or sperm cells, or of the parents that produce them, exercise more or less control over the sex of the offspring.

Environmental Factors That Determine Sex.—Certain instances might be cited to show that environment exercises more or less control over sex. Every animal begins its life with a certain genetic constitution which to some degree determines its sex, but many species may change from one sex to another in response to environmental changes. Cladocerans may continue for generations to reproduce parthenogenetically, but crowding or extreme temperatures will cause males to appear. Banta and Brown (1932) believe this to be due to changes in the viscosity of their protoplasms as well as changes in chromosomes brought about by crossing over. Metabolic level and chromosome complex may both be effective in determining which sex is produced (Muller 1932, Riddle & Bates 1936, Shull 1925, 1929). Certain molluscs which are essentially sessile (Crepidula, Teredo, Ostrea, Venus) give excellent examples of the effects of environment on sex. Such snails and clams typically pass through three phases: at first functionally male, then female, and perhaps finally male again (Gould 1917, Coe 1936, 1936*a*, 1936*b*, Loosanoff 1936). But phases may be omitted if environmental stimuli are effective. For example, if a number of crepidulas settle down together, some of them may become females at once without

passing through a male phase. If a large male and a small male are placed close together, the large individual soon becomes functionally a female. Thus the sex of these molluscs is influenced by the sex of their neighbors. The sex of rotifers, cladocerans, aphids, and other animals may be influenced by environment (Shull 1929). Temperature, food, excretory products (Stuart, Cooper, & Rose 1932), and other factors may influence sex or sex ratios.

Evolution of Sex.—Seton (1909) and Geddes and Thomson (1914) have discussed the evolution of sex in the animal kingdom. These authors believe that animals were at first sexless, then hermaphroditic and mated promiscuously; that further development led to polyandry, polygamy, and finally to monogamy. Seton argues that monogamous animals will always surpass others in the struggle for existence.

Secondary Sexual Characters.—Secondary sexual characters have excited much discussion among naturalists, and a number of theories have been proposed to account for their origin and development. There have been strong advocates of natural selection and of the effects of use and disuse as factors in the development of secondary sex characters. Recent discussion has centered largely around the actions of hormones and differences in metabolism between males and females. There is no doubt that certain secondary sex characters appear when hormones are secreted (often as gonads mature) and that they can be induced under experimental conditions by the injection of hormones. Cyclical seasonal changes in birds, for example, are controlled by gonadal and other hormones and may be modified under experimental conditions (Witschi 1935, 1936). Some males are known to show characteristic differences in metabolism from females of the same species. The symmetry of alpheids and fiddler crabs, which show striking sex differences, may be changed by irradiation and other procedures that change metabolism, and sex intergrades may thus be produced (Darby 1935, 1935*a*). Examples of striking differences between males and females among domestic fowls are familiar to everyone. Similar instances might be cited among worms, crustaceans, spiders, insects, fishes, amphibians, reptiles, birds, and mammals. Hudson (1913) points out that moths having semiapterous females and flying males are commonly associated with a widely distributed food

and that they usually appear early in the spring, when low temperatures make extensive flights undersirable. Montgomery (1910), in his consideration of the mating of spiders, lists six types of secondary sex characters: (1) weapons employed by males in their combats with one another; (2) characters used for sexual recognition and sexual stimulation; (3) characters of more immediate value in insuring approximation of sexes and copulation; (4) characters of value in provision for, and for the nurture of, the progeny; (5) characters associated with differences in habits between the sexes; and (6) characters of especial value

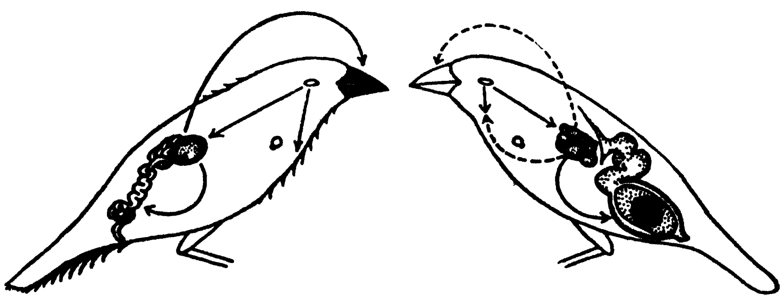


Fig. 117.—Diagrams representing hormonal relationships in African weaver finches during the breeding season. In the male Promelana on the left the active hypophosis releases gonadotropic hormones which induce the development of nuptial plumage and the growth and maturation of the testis, which in turn releases the "male sex hormone," stimulates the epididymis and vas deferens, and causes the deposition of black pigment in the beak. In the female Quelea on the right the gonadotropic hormone stimulates growth of the ovary and leads to maturation of ova and ovulation. The activated ovary releases oestrin, which stimulates the oviduct but inhibits the deposition of beak pigment and offsets action of hypophysial hormone on the plumage. Arrows in full line indicate stimulation; in broken lines, inhibition. (*From Witschi* 1936.)

in protecting a particular sex against other species. Secondary sex characters are usually qualities that are present in both sexes but are developed to a greater degree in one than in the other. Goldschmidt (1923) has made a comprehensive study of "the mechanism and physiology of sex-determination." He states that secondary sex characters may be produced through hormones from a centralized gland (hormonic) or from tissues generally distributed through the body (genetic). In either of these cases sex transformations or sex intergrades may be produced by destruction of glands or inhibition of secretions. In moths, Goldschmidt has been able to produce all degrees of intersexuality experimentally.

Mating Activities of Animals.—The activities associated with reproduction that relate to the environment and to objects outside the bodies of the animals performing them are often manifest long before the fertilization of the egg and may continue for years after the young are able to shift for themselves. Many animals carry on an elaborate courtship as a preliminary to mating. At the breeding season there is a sexual urge, or desire to mate, which in many cases is brought about by the presence of internal secretions. Various special adaptations, both structural and behavioristic, which are apparently related primarily to courtship, have been developed. It is desirable for a male or a female to possess certain apparent characteristics which render sex readily and indubitably apparent to individuals that need mates. In addition to qualities that make the discrimination of sex quick and easy, there are often those which make one sex attractive to the other, so that it is actively sought for, and those which stimulate the performance of acts that are essential for reproduction.

Animals That Depend Largely on Touch for Mating.—There are animals that depend largely on touch stimuli during their mating activities. Chidester (1911) after studying four species of crabs concluded that sex discrimination was largely accomplished through tactual stimuli and that "opportuneness of proximity" was the chief factor in mating. During the breeding season males were restless and moved about continually; females were rather passive and awaited the visits of suitors. McCook (1890) and Montgomery (1910) agree that snare-weaving spiders depend largely on touch during their mating. A male seeks out the web of a female, timidly takes up his position at the margin, and sends signals in to his prospective mate by shaking the threads. If the female is ready to mate, she may permit him to approach; but if she is not, she quickly chases him away or catches and devours him.

Animals That Depend on Odor for Finding Mates.—Moths depend largely on odor for finding their mates. The males usually seek out the females and usually approach them against the wind (Webster 1903). The males of certain butterflies have glandular brushes on their abdomens. They fly about in sunny patches in sheltered spots, and females come to them against the wind (Latter & Eltringham 1935). Several investigators have

shown that a marked male moth is able to find a concealed female, even when it has to travel a mile or more. Green (1919) in speaking of the cladoceran, *Simocephalus vetulus*, says:

> Sexual attraction is limited not only to sexual females in the sexual state, but is confined to a limited period of a few hours before the ephippial egg is laid. It seems to be due to some kind of substance emitted by the female and borne by her exhalent respiratory current, where it is detected through a chemical sense by the male.

The males of solitary carnivores (marten, cougar) commonly distribute "signs" on their hunting grounds during the breeding season, so that visiting females may know that the areas are occupied by males.

Animals That Depend on Sounds during Mating.—Certain insects and vertebrates make considerable use of sounds during mating. This is especially true of nocturnal species and those that are concealed—the call of the whippoorwill and cricket are familiar to everyone. During the breeding season many birds are accustomed to sing or call from conspicuous perches. Some birds resort to "singing trees" (Mousley 1921) or other favorite situations for their singing. Hawkins (1920) believes that bird songs serve primarily to arouse sexual excitement, not to win mates by their aesthetic appeal. Certainly they often serve to give notice that territories are occupied and will be defended against trespass. Among grasshoppers (Isely 1936) and crickets (Fulton 1933, Shull 1917*a*) songs undoubtedly serve to give notice of the location of individuals that seek mates.

Animals That Depend on Visual Stimuli for Mating.—Among animals that depend largely on visual stimuli for finding mates the fireflies are excellent examples. The males fly about flashing their lanterns at a rather rapid rate; the females sit in the shrubbery and glow at intervals. There is no question that the lights serve as signals for finding mates (Mast 1912*a*, Buck 1934). Certain marine annelids make use of luminescence for mating in much the same way (Galloway & Welch 1921). Among diurnal vertebrates use is commonly made of colors and peculiar patterns for the discrimination of sex. Male fiddler crabs appear to make use of colors in mating. The males stand at the entrances of their burrows and wave their bright-colored claws to attract the atten-

tion of the females (Pearse 1914*a*). Folsom (1923) does not believe that insects make use of color discrimination in mating. Some insects, however, undoubtedly depend primarily on vision for finding mates. The males of the flies of the family Dolicopodidae have little flags on their front legs. They walk about on leaves and wave their signals to attract the attention of females. Noble and Curtis (1935) have demonstrated a very fine example of sexual selection in fishes. They placed a female cichlid (*Hemichromis bimaculatus*) in a glass aquarium. This was surrounded by other aquaria which contained males in various stages of nuptial coloration. The female always laid her eggs on the side of her aquarium nearest the brightest colored male. Another fish (*Lebistes reticulatus*) used bright coloration to enable males to avoid one another during the breeding season. Lizards also use bright and striking colors as intimidating devices in maintaining territories against rival males (Noble & Bradley 1933).

Mating Activities.—Animals resort to various means to secure mates. Courtship often takes elaborate and peculiar forms. It serves not only to insure the formation of zygotes and thus keep species in existence but by selective mating may tend to segregate animals into races and may thus contribute to the origin of new species. Among protozoans, molluscs, crustaceans, insects, and other animals individuals have been observed to mate with others that resemble themselves in size, color, or other qualities (Crozier & Snyder 1923). Certain field crickets segregate into races on account of differences in songs, and different types "seldom if ever interbreed under natural conditions" (Fulton 1933). The immediate purpose of courtship is to secure a mate. This may involve fights between rival suitors, the demonstration of sex, and the stimulation of desire to mate. Usually males are most active, but females sometimes take the initiative. Huxley (1923) maintains that among most animals females have a lower level of sexual emotion than males and require special stimulation before coition. He believes that too frequent coition is thus prevented. Simpler types of activity associated with mating have now been considered; examples of courtship among arthropods and vertebrates will next be discussed briefly. Pyecraft (1913) has written a popular book on this subject.

Courtship among Insects.—Male tiger beetles are usually more active than females, but in the absence of a mate either sex may become active. Prevention of normal reproductive activities increases the death rate among them (Tower 1907). Hancock (1905) has described the courtship of a tree cricket. The male approaches the female with wings upraised and sings loudly. He also has an "alluring" gland on the dorsal surface of his thorax, and the female mouths this over while mating. Among mantids both sexes are carnivorous, and females frequently attack and devour the smaller and more active males. "Fertilization is assured by the stealthy approach of the male, and his whole behavior during courtship is such as not to attract the attention of the female" (Roeder 1935). If the male is attacked and killed, copulation may still take place, for the movements of the genital appendages are controlled from the last abdominal ganglion. Perhaps the most unusual example of the evolution of habits of courtship in insects is among the empid flies. Among primitive empids males capture small animals, such as insect larvae, and offer them to females. If a female accepts the attentions of a suitor, she devours his offering while mating. Some male empids spin cocoons about the presents that they submit to females. Among the most specialized empids, males execute a dance on wings before the female while spinning a cocoon. These ornate, spinous, empty capsules are offered to prospective mates. They are quite empty.

Courtship among Fishes and Amphibians.—There are many examples of fishes that assume bright nuptial colors and carry on various types of courtships. As has been pointed out, colors perhaps more often function to give notice of sex than to "attract" mates, but some males spread their fins and display their colors before females. A horned dace carries stones in his mouth and constructs a crude nest, in which he solicits passing females to lay eggs (Reighard 1890). A breeding male palmate newt is brightly colored and has a prominent dorsal frill and a filament extending beyond the tail. He places himself in front of a female, bends his tail toward her, and vibrates it rapidly. If she turns aside, he moves in front of her again; but if she stops, he deposits a spermatophore which she often picks up (Cummings 1910, 1911). The songs of frogs and toads during breeding periods are familiar to everyone. They give notice of the pres-

ence of individuals, ready to breed and established in favorable situations. Male salientians have a strongly developed clasping reflex, which is controlled in the brachial region of the spinal cord. They will clasp almost any object that moves near them while in ponds during the breeding season.

Courtship among Birds.—Many male birds, *e.g.*, house wren, American robin, continue to sing and in other ways pay attention to the females throughout the breeding season, thus apparently stimulating her to continue the usual activities in the reproductive cycle. Continual singing also serves to give notice to other birds that a particular area is already occupied by a nesting pair. The red-throated diver, according to Huxley (1923), continues its courting behavior after pairs are mated for the season, and the displays are similar in both sexes. The female European cuckoo is often pursued by as many as eight suitors; the males in summer appear to frequent definite areas and call for mates (Woodruffe-Peacock 1910). A male marsh hawk displays his agility before his mate by performing "loops" in the air. Males and females that mate and continue to consort together while rearing young commonly make some division in the necessary labor. This perhaps reaches its climax in the Indian hornbill. The male seals the female up in a hollow tree where she can brood in safety and wears himself thin seeking food for her and the young. Huxley (1912) has made careful observations on the behavior of the redshank during the mating season. The cock pursues the hen on the feeding grounds, following her about persistently. When thus attended the female usually runs or flies; but if she stops, the male begins his display. He raises his wings and vibrates them rapidly; sings; and steps high with his feet. He also makes "love flights" above the breeding grounds, performing peculiar antics on the wing, and frequently calls from conspicuous situations. The godwit (Fig. 118) carries on similar breeding activities (Huxley & Montague 1926). Phalaropes are peculiar in that males incubate eggs and the females perform functions usually assumed by male birds. The females of the red-necked phalarope reach the breeding grounds before the males and fight over each male as he arrives. The male courts the female and leads her toward a definite nesting site which is in the area that she is defending from encroachment by other mating pairs. The male takes a

leading part in the care of the eggs and young (Bahr 1907*a*, Tinbergen 1935*a*). During the breeding season a male flicker intimidates rivals by peculiar calls, head bobbing, uptilted beak, and wing and tail flitting to expose bright colors. He has a "moustache" which gives notice of his sex. A female that had an artificial mark of this sort placed on it was attacked by her mate (Noble 1936). Some birds resort to regular courting grounds during their breeding season. For example, the males of Gould's manakin assemble in groups, and each clears a small space on the floor of the forest. Such areas are recognized as definite mating territories. When a female approaches, each male occupies his own court, makes displays, gives calls, and



FIG. 118.—Male godwit sitting on eggs. (*From Huxley & Montague* 1926.)

may be joined by her in a dance and finally copulate (Chapman 1935).

Courtship among Mammals.—During breeding seasons female mammals usually are much sought by males who are attempting to secure mates. Male moose and other ungulates bellow through their own territories and fight one another when they meet. Carnivores which occupy and jealously guard separate territories tolerate members of the opposite sex during mating periods. Primates show characteristic differences in mating behavior: male baboons fight for females and maintain autocratic control over their harems; howler monkeys are very tolerant, and a female in a group may mate with several males (Carpenter 1934, Yerkes 1935).

Contests for Mates.—Among species where there is rivalry for mates, the members of the aggressive sex, which is usually the male, often fight among themselves. Male tree crickets fight in the presence of females. Male running spiders commonly engage in combats during the breeding season. After a swarming flight,

a male termite attempts to drive away all others from the female that he is following. Male penguins fight fiercely, and the winner then courts a female. Many other instances might be cited (stag, grouse, alligator, salmon, beetle, etc.). Darwin (1859) believed that such combats during the mating season resulted in the selection of the better individuals by the sex being contested for, because it chose the victors, and that the race thus progressed. There are many cases in which males actually fight to hold mates, and these are particularly clear-cut among polygamous animals, such as seals and certain ruminants. There are other cases, however, where the winning suitor is not always chosen as a mate, but the loser is often favored. Such combats (grouse) apparently serve only as a part of the activities that bring the more passive sex to a state of sexual excitement.

GREGARIOUS, COLONIAL, AND SOCIAL ANIMALS

Aggregations.—Animals collect in more or less permanent groups for various reasons. The chief activities that bring animals together are associated with protection from enemies, breeding, and feeding (Parr 1937). Some animals of the same or of different species resort together in circumscribed areas chiefly because they are dependent on habitats that are limited in extent (Fig. 119). Other groups seek to associate with each other. Colonies are made up of animals that are actually connected together, at times even by a common flesh or skeleton, or attached to a substratum in close proximity. Often they are produced by the budding of a single individual. Societies consist of animals that are independent individuals, as they are able to move about separately but live together with more or less interdependence and cooperation because there is some degree of division of labor among them. Many animals are brought together by responses to changes in environment. Sometimes such aggregations are seasonal and may be induced by changes in temperature, visual stimuli, changes brought in water by the presence of living organisms, and various other causes. "Once formed, aggregations of aquatic organisms condition the medium surrounding them by the addition of secretions and excretions" (Allee 1934*a*). Snakes show aggregative tendencies and are less active metabolically when in groups than when isolated (Clausen & Mofshin 1936, Noble & Clausen 1936, Prater 1933). Fishes show similar

tendencies (Allee 1927, 1934*a*, Langlois 1936). Even certain terrestrial insects show aggregative tendencies and are influenced to form groups by chemical stimuli in their environments (Garbowski 1935). Extensive schemes for the classification of aggregations have been published by Deegener (1918) and Allee (1931*a*). They differentiate accidental groups from "essential aggregations" or societies. The latter group is subdivided into homotypical and heterotypical societies; and these include over 50 different types of groups.

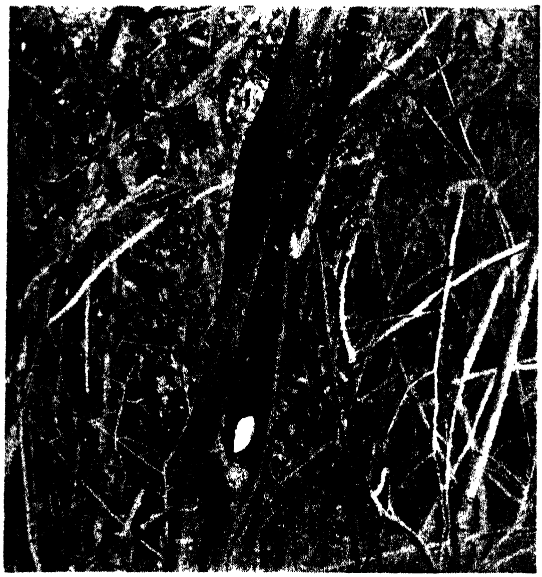


FIG. 119.—Desert snails aestivating in the twisted trunk of an acacia tree, Colombia.

Gregarious Animals.—Some gregarious animals are hostile to each other. Fiddler crabs fight continually, and one is very quick to attack another which invades the preserve about the mouth of its burrow (Pearse 1914*a*). Herring gulls on their crowded nesting areas are quite quarrelsome, the adults and larger young often killing the smaller birds. Each parent has a strongly developed instinct to guard its nesting precincts (Strong 1915). Longley (1918) found that a burrowing fish (Gnathypops) near Tortugas was commonly found in colonies and says that the distribution of this species is "probably in part due to the discontin-

uous occurrence of suitable bottom rather than to the social instincts of the fishes themselves." Nesting ibises of two species occupy a considerable swampy area in Australia, where their nests are closely crowded together and favorable spots are occupied by groups of young and their attendant nurses. In another part of the same swamp, spoonbills and little cormorants nest together. Both these breeding grounds are occupied by the same species year after year, though they are apparently not essentially different from other available areas. These birds apparently have a place association, or homing instinct, in relation to a particular area (D'Orbain 1906). The albatrosses show similar relations to Laysan Island, where a million are estimated to breed. Their young eat 600 tons of squids per day. Each mother appears to recognize her own young and pecks others that solicit food from her. The wood rat in Oregon forms groups that build great nests in trees. Each rodent is separated from other individuals by a partition, but all run about the common nest freely and are more or less tolerant of each other (English 1923). Such animals as have been mentioned are apparently gregarious because they are associated with areas that are particularly favorable or particularly favored by the species concerned. Some animals show more or less gregariousness of a type that has no particular reference to areas but relates primarily to individuals. In such groups of animals there are bound to be certain disadvantages and certain advantages for individuals. Competition is keenest among members of the same species, and a gregarious animal lives in the midst of fellows that are jealous of every success. On the other hand, a group is more likely to receive notice of danger than an isolated individual, and some species (prairie dog, flamingo) commonly give warning calls when an intruder approaches. Herds of elk and deer are able to ward off attacks of large carnivores by associating together. If animals are close together it is easy to find a mate, and even the choice of a particular type of mate is possible. Tiger beetles are not gregarious or social, but frequent restricted areas and different species have been observed to attempt to mate with each other (Shelford 1911).

Gregarious Predators.—Many predaceous animals form groups for hunting. The individuals of a group may be more or less jealous and intolerant toward each other, but, having a common desire for food, they are willing to cooperate in securing it. A

buzzard dropping down to its meal is observed by its keen-eyed fellows which soar at a distance, and within a few minutes after the death of an animal many of these birds may be feeding on the carcass. Lions may hunt singly but usually go about in small groups, consisting of a male and two to four females, and Selous (1908) has observed as many as 20 together. Wolves commonly hunt in packs and are thus able to kill animals that are larger and stronger than themselves. Insectivorous birds commonly fly in flocks and are probably thus able to capture agile insects which might be able to escape from a single hunter. Widman (1896) pointed out that birds with long wings are more often gregarious than those with short wings, apparently because they are able more easily to cover long distances for feeding and roosting. He also states that birds of different species often go about together in flocks and that among passerine birds only assassins, like the shrike, are habitually solitary. It is "not safety from enemies which makes birds congregate."

Gregarious Migrators.—Many species of birds commonly congregate into flocks after their breeding season and migrate together. Whittle (1923) has presented some evidence that certain flocks of birds are relatively permanent associations of individuals that have bred in the same general locality and have migrated together. Some young animals are very gregarious. Many young fishes commonly swim together in schools, and some continue to do so throughout their lives (Meek 1916, Snyder 1922). Gibson (1903) has described the behavior of *Hyperchiria io* caterpillars, which feed together side by side under leaves, and tent caterpillars, which are gregarious when not feeding. Cenethocampa caterpillars build nests in pine trees and migrate in processions. The leader of the procession changes from time to time, and all individuals seem to have a strong instinct to follow a temporary leader (Brindley 1910). The spiny lobster is gregarious (Crawford & Smidt 1922). Several individuals may crawl about on a rock, the antennae of one touching the body of the one in front of it. On the coast of Japan enormous swarms of stomatopod larvae are encountered at times (Komai 1932).

Social Life Not Commonly Derived from Gregariousness.—Though gregarious animals have in many instances a tendency to coöperate to some extent and to make some division of labor

among themselves it is proper to say that such associations have rarely if ever led to a high degree of specialization in communal life. The specialized societies have largely grown up out of families. The tenacity with which the members of extensive and crowded groups of animals, such as those found among aphids, fiddler crabs, barnacles, and mussels, cling to their individuality indicates that mere living together does not necessarily lead to social life. Parents have instincts that often make them tend to foster and cherish their offspring. These make it easy to continue family groups and expand them into clans or larger societies (Legewie 1931).

Colonies.—Colonies occur among species of animals that are attached and have, by an extension of natural growth processes, formed a more or less loosely organized group of individuals which is organically connected and often shows a considerable degree of specialization along the line of division of labor and cooperation for the good of the whole group. Sponges form loose colonies which are without much unity. Individuals are hard to segregate and may be fused or separated without greatly interfering with the parts. Some colonies, such as barnacles on rock beaches (Fig. 54), are formed by the attachment of sessile animals in favorable situations. There is no cooperative activity or interdependence among individuals in such groups.

Correlation between Members of a Colony.—In coelenterate colonies individuals are usually connected by a common flesh. There is often more or less polymorphism and alternation of asexual with sexual methods of reproduction. Division of labor among the members of a colony may be carried to a high degree. Brooks (1885) has discussed in a masterly way the origin of metagenesis and polymorphism in coelenterates, and his ideas will be presented in the next two sections in this chapter. The individuals of the sea pen (Renilla) in their withdrawals and expansions show no particular coordination or sequence, but the peristaltic waves which pass over the peduncle and the luminescence are unified activities which are characteristic of the colony as a whole. Bryozoans and ascidians show more or less division of labor among the individuals in their colonies. Van Name (1921, 1921*a*) maintains that simple ascidians probably came from colonial ancestors which were obliged to give up budding habits because they became too large and complex when they

took up a free-swimming existence. He thinks it possible that the ancestors of the vertebrates may have been colonial. Williams (Allee 1919) found that when a bryozoan colony (Pectinatella) was starved it lost one individual after another and the whole colony did not die at once. In all cases of division of labor among colonial animals the segregation of activities is so bound up with polymorphism that it may properly be left for discussion in the next section.

Social Life.—As has been suggested, social life rarely, if ever, arises from the chance association of individuals of a species, and a high degree of social specialization always grows out of relations that are primarily those of the family. Social life is dependent on cooperation. Lowie (1920) in speaking of human society says: "Biologically every community must rest on the family," and Wasmann (1913) makes similar statements concerning ants. Kropotkin (1916) has emphasized the fact that food necessities tend to make animals competitive and antagonistic and that reproduction tends to bring them together. The burdens laid on parents in bringing forth and rearing young have in many cases led to far-reaching results in the way of cooperation, the lengthening of life, the production of food and the maintenance of food resources, and even intellectual life. In well-organized social life there must be continual compromises between selfish instincts and those that are for the good of the community. Lameere (1922) holds that the social life of ants saves the race from extinction because the worker individuals continually seek for food and continually regurgitate it to their fellows, thus supplying the reproductive individuals. Steiner (1924) has stressed warmth as a factor in the development of social life and claims that animals cannot cooperate effectively unless they are able to maintain a high body temperature over long periods of time. The effects of aggregation on the ability of fishes to learn and carry on ordinary activities has been studied by Welty (1934). "The group seems to stimulate learning behavior in three related ways: through group cohesion visually integrated; through an inter-'reassurance' which tends to remove environmentally induced inhibitions; through an interaction between members of a group which stimulates exploratory activity." A goldfish learns to run a maze more quickly if it sees other goldfishes do it, and groups retain conditioned responses more readily than individuals.

Social Insects.—Wheeler (1923, 1926) in his incomparable way has discussed the social life of insects. He points out that tendencies toward social life were present as far back as the Carboniferous period and that ants were socially in about their present state at the beginning of the Oligocene, some 50,000,000 years ago. He asserts that social habits have arisen twenty-four times in more or less distantly related families of insects and in every case through the prolonged association of a mother (or of both parents) with eggs and young. The social habits of insects have their origin largely in the propensity of females to lay their eggs on or near food that is suitable for the hatching larvae. Some parents further remain with the eggs and young until they are able to shift for themselves; some actively seek and store food for their coming offspring. When the adult stage is lengthened so that parents may have prolonged association with one or more generations of offspring, a high degree of social life becomes possible. The societies of insects differ from those of man in that they lack "time-binding" elements, such as books and inventions, which civilization carries along in a cumulative way in succeeding generations.

In the termites and all the beetle groups the colony consists of a male and a female parent and their offspring of both sexes; in all the Hymenoptera, Dermaptera, and Embidaria the female alone founds the colony, which is developed by her daughters. The former groups are, therefore, gynandrarchic, the latter gynarchic.

Ants, according to Wheeler, are the dominant insects on the earth, probably exceeding all other insects in numbers. Their dominance is due in large measure to their social life. Like the societies of man, theirs have passed, and are passing, through hunting and pastoral stages, but many have now attained a high degree of development. Most ants feed only on liquids and continually practice trophallaxis (mutual feeding), which tends to spread all available food throughout the community. Ant communities vary in numbers "from dozens to millions."

Termites have excelled ants in the construction of elaborate nests (Fig. 120) which control temperature and humidity, give protection from predators and harmful fungi, and thus enable the termites "to live in otherwise uninhabitable niches" (Emerson 1938). Their nests have evolved from mere cavities in wood to

extensive underground tunnels and gigantic mounds. They are equipped with covered tunnels and roads, rain-shedding projections and ridges, ventilation apertures in walls, granaries, and fungus gardens. All these are made possible by a complicated and specialized social organization. A general review of social insects has been published by Maidl (1934).

Social Birds.—Birds show all degrees of social organization. Among some species individuals are usually intolerant of others but flock together during migratory flights (plovers) or breeding



FIG. 120.—Termites' nest, shaped like a toadstool, Nigeria.

seasons (albatross). Some birds are more or less gregarious and social the year round (Fig. 121); pelicans nest together in great rookeries and commonly fly about and fish together at all seasons (Coker 1919). Among a number of species of birds in Guatemala several individuals sleep together in one nest, and pairs that are rearing young are assisted by unmated helpers (Skutch 1935). In flocks of parrots, chickens, and other more or less social birds there is an order of "peck dominance" (Allee 1936, Masure & Allee 1934, Murchison 1935). In composite flocks made up of birds of different species which gather together

to hunt or migrate, certain species often take the initiative and act as leaders (Gerke 1932).

Social Mammals.—Among mammals societies reach their highest development in the case of primates and rodents (Seton 1919). A primitive society consists of a mother and a few of her offspring. When a father is also a member of a group, social life is on a higher level. In herds of ungulates the males are usually brave and pugnacious. They are quick to defend their society against danger. When a herd of bison is attacked by enemies the bulls form a ring with the cows and calves within



FIG. 121.—Social weaver-birds' nests in oil palms, Nigeria.

and thus fight their battles. Male rodents are often aggressive in defending feeding areas. In primate societies groups are usually made up of one or more families. Howler monkeys wander through treetops over definite territories. Several males and females live together amicably. When danger threatens, any male may lead the others; there is no permanent leader (Carpenter 1934). Chimpanzee groups seldom include more than a single family with perhaps an added young male. The father of the group dominates it. Baboons often travel in large bands, which may sometimes number hundreds of individuals. Within these there are very definite family groups. The dominant male

is very pugnacious and domineering over young males and females in his clan. Often baboons are killed in fights over females, territory, or food. When danger threatens, the oldest, strongest males act as sentinels or rush to the point of attack and fight bravely. A male howler monkey is a comparatively meek and mild socialist; a chimpanzee is devoted to his family affairs and attends to duties connected with them; a baboon is a fighting, intolerant autocrat who treats his wives and attendant young males with little consideration (Yerkes 1935).

Division of Labor in Societies.—The division of labor among social animals usually tends to develop specialists for reproduction, foraging and feeding, and defense. A community has a certain unity because its individuals are interdependent and cooperative. Wheeler (1911*a*) has discussed an ant society as an organism. He first classifies "persons" of different grades as (1) protozoans, (2) simple nonmetameric persons, (3) metameric persons, (4) primitive colonies, (5) families or colonies of reproductive type, (6) coenobia, (7) true or human societies. He likens an ant community to an organism because it has individuality, soma (workers and soldiers), and germ (queen). It may live 30 to 40 years and carry on "asexual reproduction." Workers serve primarily for provisioning the community but also retain their nursing instincts. Wheeler (1907) says: "Instincts relating to the nurture of the young bear the aspect of a dominating obsession." This makes the entrance of guests and parasites into an ant community comparatively easy. Some ant queens cannot establish a new colony without the assistance of workers. In some species minute workers cling to a female that is making her nuptial flight and are thus at hand to assist her in establishing her new home. Soldiers, according to Wheeler (1911*a*), have "fear and rage" instincts specialized, and some perform very special duties. For example, in the genus Colobopsis, which bores in wood, certain peculiar individuals stand at the entrances of dwellings and use their bodies as living stoppers. The heads of these soldiers completely close the entrances. If a member of the colony attempts to enter, the doorkeeper stands aside, but all other solicitors are excluded (Wheeler 1904). In beehives certain individuals serve as sentinels and turn back all strangers at the entrance. Lameere (1922) holds that reproduction is limited in social insects

to prevent overpopulation. The ability to reproduce is limited to a few individuals, and in many cases the brood is destroyed or devoured by members of the community if there is a scarcity of food. On the other hand, an ant queen that is deprived of her first brood will rear another; this is a remarkable instance of regeneration. Uichano (1919) studied a Philippine termite which raises fungus for food. The male and the female build the nest together, and the latter may live perhaps for as long as 20 years. Some termite soldiers not only bite but also throw out from their heads a sticky secretion which entangles enemies. Hopkins (1898) has shown that female wood engraver beetles help each other in making excavations in soft wood. One gnaws away the wood while the other pushes out the shavings. They prepare beds for rearing ambrosia fungus, which is their chief food. A chamber is set apart for the bodies of dead beetles and other undesirable objects. In some species of these beetles the males are wingless and few in numbers. In such cases the females stand guard at the entrance. Among other species, in which males and females occur in approximately equal numbers, the males act as guards, often spending their lives watching the entrance and dying there. Holmes (1922) has attempted to classify social behavior as chiefly sustentative, protective, and ameliorative. He gives various subdivisions under each of these headings.

Cooperation in Societies.—In social life division of labor must ever be accompanied by cooperation, and often this is carried to remarkable extremes. Robaud (1911) has given an interesting account of the specialization of the maternal instincts of wasps. In primitive species food is collected and sealed up with the eggs. Some wasps remain with the eggs and assist the larvae in feeding; a step above this condition are wasps that give the larva its entire food from day to day; and at the top of the series are the wasps that give their larvae specially prepared food from day to day. Robaud believes that maternal instincts represent an equilibrium between hereditary habits and physiological necessities. Wheeler (1923) has made it plain that the social life of insects and their relations with foreign animals that invade their homes depend largely on trophallaxis. The instinct to regurgitate food when solicited by a fellow is so strong that an ant that is practically starving will sacrifice food. Social

insects that gather food commonly gorge themselves when they can; they often store and use food with great economy. Mann (1913) quotes Cornetz as denying that ants show any real cooperation in carrying food to their nests; the presence of food is believed to excite the homing impulse in each individual. Other evidence indicates, however, that ants cooperate to such a degree that a returning worker can indicate to its fellows



FIG. 122.—A female chimpanzee grooming another. (*From Yerkes* 1935.)

whether few or many workers are needed to carry in a discovered supply of food (Hingston 1920). Passalid beetles modify wood before feeding it to their larvae and stridulate to keep their groups together. In wasps there is mutual exchange of food between larva and worker, but bees do not obtain food from the young that they attend.

Cooperation is not only concerned with the division of available food but often reaches a high degree of specialization in other respects. Ants assist each other in many ways—lick and clean their fellows, carry the injured, etc. Uichano (1919) found no guiding or directing individuals in termite societies but excellent

cooperation. Toleration in ants in some cases permits the mixing of different communities (Von Natzmer 1913; Wheeler 1911). A queen ant is not hostile to young queens in her nest, as queen bees are. Social spiders in India live together in groups of 40–100, repairing their common nest and feeding amicably together from the bodies of captured animals (Jambunathan 1905). In a troop of monkeys the patriarch, usually the largest male, "exerts authority, maintains discipline, interferes in quarrels, chastises offenders, settles family disputes" (Hingston 1920). Female primates (Fig. 122) commonly clean one another and their children. Gain (1913) gives an excellent picture of social life among penguins. During the breeding season there is great rivalry for nests among Adélie penguins. "Quarrels over ownership increase; each works for itself; selfishness is master; everywhere is distrust." Watchful care is continually necessary to prevent the stealing of materials for nests. But after the young appear there is great rivalry among adults to brood and care for them. They are herded and watched over by sentries which keep away the skua gulls. The emperor penguins do not build nests but hold their eggs on their feet. They fight with each other for chances to incubate eggs and to brood or feed young. Cooperation is always essential in society.

Advantages of Social Life.—The advantages of social life are many, but there are also inherent disadvantages. Cooperative activity makes the securing and conserving of food and the defense of the community easier. The association of adult oecophyllas with their larvae permits them to take advantage of the spinning ability of the latter and use them as shuttles for weaving threads to bind the nests together. Close association between individuals gives opportunity for learning. The life of social insects appears to be guided largely by instinct, but among the higher vertebrates there is more or less learning by imitation and training. Communication by the use of language of various types is also a product of, and an asset to, social life. A social system may have a span of life that far exceeds that of the individuals that compose it. Ant societies may exist for 30 or 40 years. Branner (1912) estimates the number of individuals in the nests of leaf-cutter ants as varying from 175,000–600,000. A queen termite during 10 years may lay 100,000,000 eggs. Wheeler (1923) notes that termites as a result of social

life have shown a tendency to deteriorate in their physical prowess but tend to a higher degree of nervous organization. He also observes a similar, though less pronounced, tendency in ants. Social life makes the keeping of domesticated animals and the pursuit of agriculture easier, thus rendering food resources more stable. It enables animals to maintain a higher temperature, so that activities are less intermittent. Every apiculturist knows that bees remain warm throughout cold seasons. Steiner (1924) has shown that certain ants also maintain a rather high temperature in their nests. Time binding, by which one generation obtains the benefits of experiences gained by those preceding it, is possible only among social animals. Ants inherit established nests, pastures, and hunting grounds. Man, with his unusual means for intricate expression through language and his great accumulations of learning and invention, has a society that is unique in possessing commercial, industrial, and intellectual aspects not found among other animals.

Disadvantages of Social Life.—Against social life there is always the argument that individuality is sacrificed. The specialization essential to cooperative division of labor leads to a certain limitation and loss of power among individuals. There is also an interdependence which may be fatal if all members of a society are not present and doing their parts. The instincts to feed, foster, and defend other individuals make easy the invasion of a society by parasites and guests. In India a moth and a mouse are regularly associated with the nest of social spiders (Jambunathan 1905). A large number of myrmecophiles and termitophiles have been described. There are many parasites in human society.

POLYMORPHISM

All through the animal kingdom there is more or less tendency toward the development of different types of individuals. Cells tend to differentiate into tissues; colonies, into functionally different individuals; etc. Huxley (1912) has discussed heterogeneity among animals with particular reference to individuality and points out that "compound wholes" which consist of many parts often differentiate within the whole into a variety of parts. Form differences among individuals within a species are often correlated with differences in habits or habitats. They find

their fullest expression among colonial and social animals as an adaptation for division of labor. Sexual dimorphism is perhaps more common among animals than any other type of individualistic differentiation, and many species show constant and characteristic differences between males and females. But there are many species, even among animals that are not colonial or social, that show two forms of one sex. For example, the males of certain Hercules beetles are horned or hornless. Colonial coelenterates, bryozoans, and tunicates furnish some wonderful examples of polymorphism, but this type of specialization for diversity of function is perhaps at its best among social insects, especially ants and termites.

Types of Polymorphism.—Montgomery (1906) has classified the intraspecific form relations among adult animals as follows:

I. Monomorphism.
II. Polymorphism:
  1. Among individuals of the same generation:
    a. Sexual dimorphism.
    b. Reproductive and non-reproductive individuals.
    c. Different types of males or females.
  2. Among individuals of successive generations:
    a. Sexual and asexual individuals.
    b. Sexual and asexual individuals which also show differentiation among corresponding unisexual individuals or among dioecious and monoecious individuals.

In this section only polymorphism among animals of the same generation will be discussed. Montgomery's classification, although valuable in indicating the general types of relations that occur between different intraspecific forms, does not conform to general usage in regard to the term "polymorphism," which to most scientists signifies the concurrent association of different forms of one species that are in essentially the same stages of their life histories.

Polymorphism as Division of Labor.—Polymorphism as an adaptation for division of labor has apparently arisen in various groups by the specialization of qualities already present. Some parts have been developed to a greater degree, and others have been more or less suppressed in the formation of particular types. Often the labor performed by a particular individual corresponds to the degree of development that it has attained. The nymphs

of reproductive forms of termites perform labor in their societies that is much like that performed by the worker caste (Thompson & Snyder 1919), and, conversely, the worker is in a sense an undeveloped individual comparable to a nymph. Two types of corals studied by Parker (1925*a*) differ markedly in behavior: Renilla, a stalked colony without a skeleton, responds as a colony; and correlation between zooids is controlled through a nerve net, but in three species of gorgonians "each zooid is in a striking way independent of its neighbors."

Types of Individuals among Polymorphic Animals.—The number of different types of individuals that may occur in a polymorphic species varies greatly. Many hydroid colonies commonly have feeding and reproductive individuals; those of Hydractinia regularly show stinging individuals as well; and some siphonophore colonies possess from five to seven types. Thompson (1922) states that among the termites of the genus Termopsis:

> Four stable castes are of common occurrence; the first form, the second form, and the third form are the fertile reproductive castes; among the soldiers the females are sterile and the males are probably also sterile. There is no true sterile worker caste.

Wheeler (1923) says that eight castes are known among termites, but there are seldom more than five or six in one species. The usual castes, which occur in both sexes, are as follows:

1. First-form adults—pigmented; eyes, brain, and frontal gland large; wings present (shed after nuptial flight).
2. Second-form adults—wing pads present; eyes, brain, and frontal gland intermediate in size; substitute royal forms.
3. Third-form adults—wingless; brain small; eyes and frontal gland vestigial; substitute royal forms.
4. Workers—unpigmented; brain small; compound eyes and frontal gland vestigial; head broad.
5. Soldiers—wingless; head large and more or less pigmented; brain small; compound eyes, vestigial; frontal gland often large.

Wheeler (1907) in his scholarly and inspiring discussion of polymorphism in ants describes 27 castes, which are largely among females. All ants, except certain degenerate, parasitic species, have a worker caste. Among primitive ants, workers

are monomorphic and have about the same size as sexually mature individuals. Wheeler discusses nine types of specialization: (1) workers are of same size and appearance as sexual forms; (2) some workers differ from sexual forms, and others are intermediate, thus forming a more or less graded series; (3) workers are dimorphic and rather constant in size, thus constituting worker and soldier castes; (4) soldiers have become extinct, leaving workers monomorphic; (5) workers have disappeared completely; (6) workers have remained stationary, and females have increased in size; (7) workers have remained stationary, and females have diminished in size; (8) female has disappeared and been replaced by a gynecoid worker; and (9) the female caste has differentiated into two forms. Among ants the female and worker castes have apparently advanced or retrogressed independently in their evolution.

Determination of Castes.—The castes of social insects have long puzzled students of heredity, and various theories have been proposed to explain how females could transmit to workers and soldiers, which do not reproduce and therefore do not have a chance to transmit their own characters, characters that they do not themselves possess. Certainly the male and female must have potentialities in their germ cells for all the characters that the species shows. The quantity or quality of food has often been cited as the controlling factor in the production of castes. Wheeler (1911), quoting Emery, says:

> The production of the worker form is held to be the result of inadequate feeding of the larva from which it develops, directly and clearly so in the wasps and bumble bees, but indirectly and obscurely in the honey bees, ants, and termites. The disappearance of the worker phases in certain small and permanently parasitic ants like *Anergates atratulus* is explained as the overfeeding of all the female larvae, coupled with their small size, and not as due to the uselessness of the worker caste.

Wheeler (1907) points out that in bees lack of food not only results in a retardation in the development of the gonads, but also causes the development of peculiar worker characteristics. A number of changes thus result from nutritional castration. Wheeler makes the following generalizations in regard to the Hymenoptera: (1) Except in the bees, the morphogeny of queens

is probably not dependent on food. (2) Workers fed on various diets may be alike. (3) A queen starting a colony may go without food for as long as 8 months, feeding her larvae, which are very small in such cases, on saliva. (4) Withdrawal of food from larvae by nurses or parasites produces worker castes. (5) A queen bee fed on "royal jelly" receives an unusual growth stimulus. (6) Pseudogynes result from starved female larvae. (7) Parasitic infestation may cause peculiar forms. (8) Some castes depend more or less on seasons and food, for some species produce workers only in summer. Wheeler (1923) says that trophallaxis is of general significance among social insects as the cause of the worker caste, the differences in size being closely correlated with the amount of food assimilated.

In the present state of our knowledge we can only surmise that the differences between queen and worker castes were originally ontogenetic and determined by feeding, as they still are in wasps and bees, but that in ants the germ plasm has somehow been reached and modified, so that an heredity basis for *caste differentiation* has been established.

Thompson did excellent work on the determination of castes in termites. She says (1917):

My final conclusion is that all termite castes are predetermined in the eggs, that some castes are distinguishable, either by external or internal characters, at the time of hatching, while others may appear considerably later in the course of development. . . . An argument against the view that termite castes are mutations is the fact that the five castes are constant in their occurrence throughout the very different and widely distributed genera of three families of termites (1919).

In her final paper Thompson (1922) says: "The castes of termites are regarded as segregants arising by Mendelian inheritance from a heterozygous parent form."

One of Thompson's captive colonies of termites lived 17 years without the production of first-form or second-form sexually mature individuals, and the passage of periods of time such as might recur in annual cycles therefore appears to be unimportant in this instance. Thompson believed (1919) that termite castes are determined by intrinsic causes and are not markedly influenced by conditions of environment. There are some facts, however, that appear to indicate that the production of castes is influenced to some extent by environment. Morgan (1907)

states that the presence of royal termites inhibits the production of substitutes. In certain Californian species of termites, soldiers and winged individuals do not appear until colonies attain a certain size; and if the number in a colony is reduced, their appearance is delayed. "There is nothing obvious in these experiments that suggests germ plasm as an important factor; rather it appears to be a question of quantitative or possibly qualitative feeding" (Heath 1931). Castle (1934) and Pickens (1932) support an inhibition theory of caste determination in termites—functional reproductives of each sex produce respectively a substance that, when eaten by the nymphs of a group, inhibits the development of the reproductive organs in the nymphs of that sex. This material is thought to be distributed throughout a group by grooming. Castle stresses the fact that conditions within a termite colony (number of individuals, castes already present, etc.) to a considerable degree influence the time of appearance and nature of new castes. By the removal or addition of a single individual, the balance of a colony may be altered so that the appearance of certain types may be delayed, prevented altogether, or caused to appear very soon. Pricer's (1908) observations on carpenter ants show that kings and queens were not reared unless at least 2,000 ants were present in a community. In this case the number of ants present seemed to exert a definite influence. Internal secretions, the "struggle between parts" of developing insects, and other factors have been suggested as possible influences in the production of castes. Wheeler (1907) says: "Nourishment, temperature, and other environmental factors merely furnish the conditions for the attainment of characters predetermined by heredity."

ALTERNATION OF GENERATIONS

Types of Variations in Ontogenies.—All through the animal kingdom there are tendencies toward alternation of generations, sometimes between different types of reproductive activity among structurally similar individuals, sometimes between structurally different types of individuals. Stockard (1921) says:

> Twinning or polyembryony may be considered a typical method of asexual reproduction, and its occurrence in mammals and other vertebrates makes the phenomenon of so-called "alternation of generations" universal among animals.

In the cases of polyembryony to which Stockard refers, the arrest of growth in one region may stimulate growth in others, just as the pinching off of the terminal bud of a plant shoot may lead to the development of adventitious buds which would otherwise have remained small. Darwin (1859) long ago pointed out that certain gall-fly larvae are able to produce other larvae asexually and suggested that an insect of a holometabolous type really performs a similar act when a larva is transformed into a pupa, which is a quite different type of individual from its predecessor. Montgomery (1906) calls attention to the fact that a starfish larva is to be considered a separate generation from the adult starfish, which it produces by budding. The whole larva is not transformed but collapses and dies; only a portion of it grows into a starfish. Such facts make it apparent that alternation among animals is not always a definite, clear-cut process like the alternation of the sporophyte and gametophyte among plants but is a rather heterogeneous group of tendencies which is manifested in various ways in different branches of the animal kingdom. In all cases, however, it is essentially a modification of simple and typical modes of ontogentic development in such a way that different types of individuals alternate with more or less regularity. Montgomery (1906) classified different types of ontogenies as follows:

Continuous:
  Orthoplastic—Direct
  Metaplastic }
Discontinuous: } Larval
  Metagenetic } } Alternation of Generations
  Heterogenetic }
  Ekdytic

In a continuous life cycle . . . every structure or part that appears at any time of somatic differentiation passes wholly over into a later structure. . . . Two kinds of continuous life cycles may be distinguished, as orthoplasis and metaplasis respectively. . . . Orthoplasis is the equivalent of what has generally been called direct development . . . metaplasis is a continuous development where the ontogeny is not at all points a further direct approximation toward the adult stage. The latter is development with a free larva, but without discontinuity of structure or process.

When development becomes discontinuous there may be alternations of sexual with asexual generations (metagenesis); there may be alternation of individuals that produce offspring from fertilized with those that produce from parthenogenetic eggs (heterogenesis); or there may in ekdytic development be structures

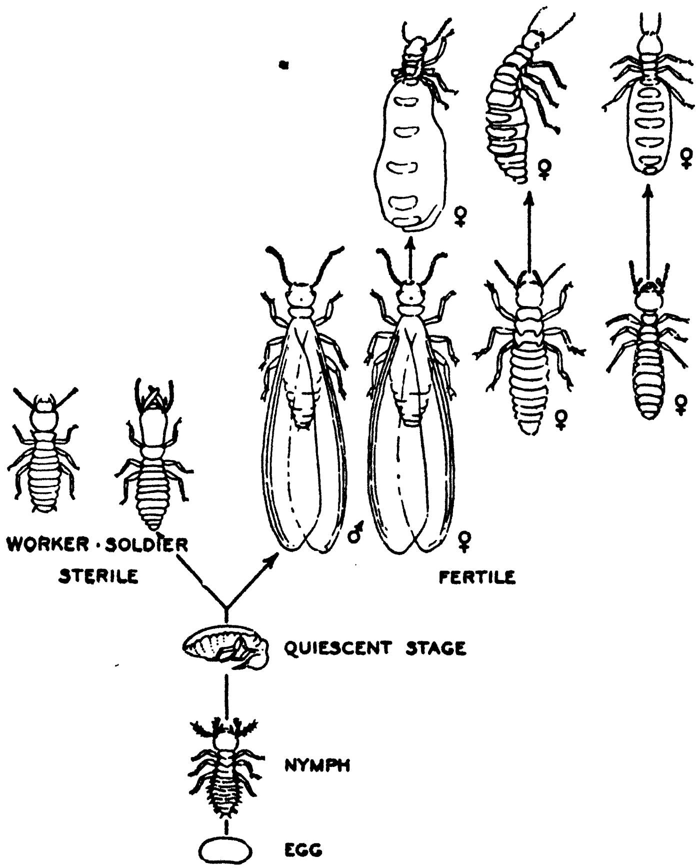


FIG. 123.—Chart to show life history and polymorphism of the termite, *Reticulitermes flavipes*. (*After Snyder* 1935.)

that serve for the protection, respiration, excretion, or nutrition of the immature animal and do not become part of the adult because they are thrown off at birth.

Ekdytic rightly interpreted includes both cases of intrauterine (foetal) development, and also any development within an egg shell where

special membranes are formed and become later discarded. This is a molt, ekdysis, of living parts.

Of the two types of alternation of generation that occur generally among animals, "all discontinuous larval development is metagenetic, in that the adult is formed asexually, by budding, from the larva," and all animals in which there is an alternation of amphigenetic with parthenogenetic individuals are heterogenetic. The starfish or the insect pupa that is formed as an outgrowth from the larva is to be interpreted as a separate generation from the larva. Heterogenesis is to be looked upon as the alternation of a complete sexual reproduction ending in fertilized eggs with a degredation of sexual processes in which eggs develop without fertilization. It is associated with an absence of males. "The probability of the occurrence of parthenogenesis seems to be proportioned inversely to the number of male individuals."

Metagenesis.—Metagenesis reaches a high degree of development among certain coelenterates and is characteristic among cestodes. Brooks (1885) has given an extensive and highly philosophical discussion of the origin and development of metagenesis in hydroids. He believes that the original ancestors of hydroids were simple, solitary, floating or swimming, hydra-like animals which gradually became better adapted for swimming and thus were modified into medusae. Later the larvae became attached to solid objects and some species emphasized sessile life so that they lost the tendency to become medusae, thus losing the chance of developing alternation of generations; but other species, as sessile polyps, developed the tendency to form new individuals by budding and by thus giving rise to medusae developed metagenesis. In many species polymorphism developed in the colonies during sessile life and this greatly complicated the life history. Brooks gives many examples that illustrate specialization toward and degeneration away from complex metagenetic cycles. The following are a few examples:[1]

Aeginopsis has a metaplastic development:

Egg—Planula—Medusa × Eggs

[1] In the life histories × indicates that one individual gives rise to another by budding or by sexual reproduction.

Cunia octinaria also has a metaplastic development, for all individuals produced ultimately become medusae:

Hydra—Medusa × Eggs
×
Egg—Planula—Actinula—Medusa × Eggs
×
Hydra—Medusa × Eggs

Cunocantha parasitica shows metagenesis because the actinula does not become a medusa, but completes its life as an individual after budding off hydras:

Egg—Planula—Actinula × Hydra—Medusa × Eggs
Hydra—Medusa × Eggs

Turritopsis shows a secondary alternation of generations:

Hydra × Medusa × Eggs
× Medusa × Eggs
Egg—Planula—Root ×
Hydra × Medusa × Eggs
× Medusa × Eggs

Eutima shows secondary alternation of generations and polymorphism:

Blastostyle × Medusa × Eggs
Nutritive hydra × Nutritive hydra
Egg—Planula—Root ×
Blastostyle × Medusa × Eggs
Nutritive hydra × Nutritive hydra

Cestodarian tapeworms have simple life histories, but cestodes commonly show metagenesis, as follows:

Proglottid × Eggs
Egg—Onchophore—Cysticercus—Scolex ×
Proglottid × Eggs

Taenia echinococcus shows a secondary alternation of generations

Proglottid × Eggs
Cysticercus—Scolex ×
Proglottid × Eggs
Eggs—Onchopore—Cysticercus ×
Proglottid × Eggs
Cysticercus—Scolex ×
Proglottid × Eggs

Certain annelid worms bud off sexual individuals from an anterior individual which does not become sexually mature. One

anterior individual may produce several others, which are all of the same sex. Chalcid flies almost attain a secondary metagenesis, for one egg may fragment into a number of individuals.

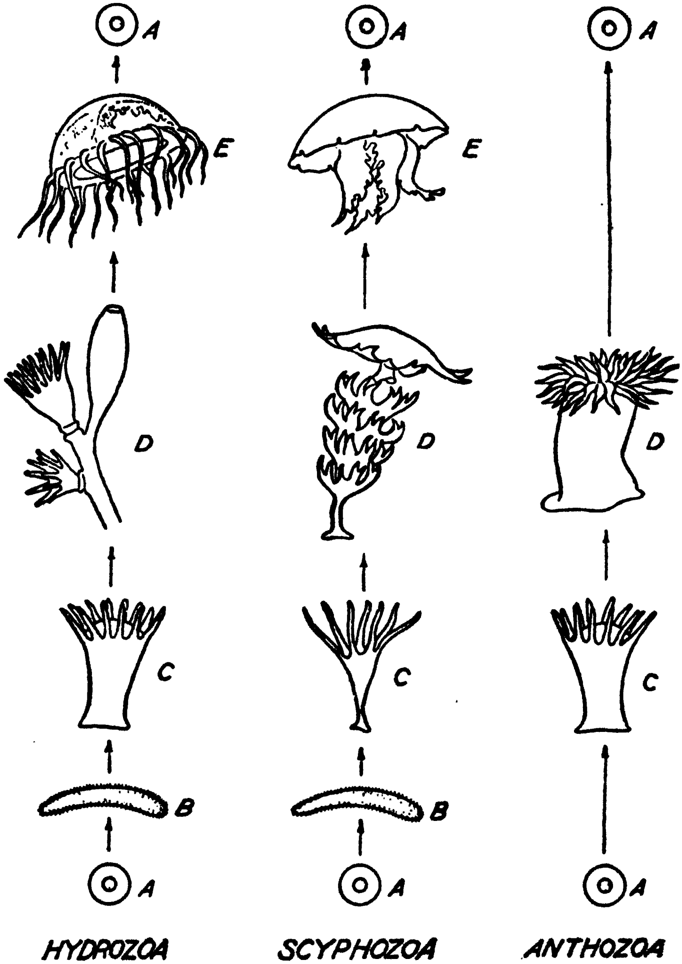


FIG. 124.—Life histories of typical coelenterates. *A*, zygote; *B*, ciliated planula; *C*, young polyp; *D*, mature polyp; *E*, medusa. In the Hydrozoa all stages usually appear in a well-developed condition; in the Scyphozoa the polyp is always small and unimportant; the Anthozoa never have a medusa stage. (*From Pearse's "General Zoology," courtesy of Henry Holt & Company.*)

Heterogenesis.—Heterogenesis is well developed among aphids, cladocerans, rotifers, certain nematodes, and digenetic trematodes. It more often shows variations in the periodicity of

different types of individuals and appears more often to be more or less directly affected by conditions of environment than metagenesis. Some species of aphids have very complex life histories.

Baker and Turner (1916) describe as follows that of the rosy apple aphis in Virginia:

Where found	Apple	Apple	Plantain	Plantain	Apple
Stage......	Stem mothers (wingless)	About seven generations of mothers (at first wingless; last generation nearly all winged)	Four to fourteen generations, mostly wingless	Winged males and females	Eggs
Time......	Apr. 8–16	May 20–June 20	June–September	October	October and November

This life cycle includes a very large number of generations, all of which are produced as living young from parthogenetic females, except the stem mothers, which hatch in the spring from fertilized eggs. Rotifers, aphids, and cladocerans pass through life cycles that are fundamentally alike (Shull 1929). Reproduction is chiefly by parthenogenesis, but at times gamic males and females occur. Gamic forms produce fertilized eggs which are capable of living over winter or of surviving through periods of drought. From the fertilized egg hatches a female that is obligatorily parthenogenetic, and her offspring are all females. Individuals in the second generation may be parthenogenetic or gamic. Some species have regularly alternating amphigenetic and parthogenetic generations; in others parthenogenesis only often continues for many generations. In rotifers a gametic female, if not fertilized, produces males from the same eggs that would, if fertilized, produce females; and females that produce either sex are much alike in appearance (Fig. 125). Among aphids parthogenetic and gamic females are structurally distinct. In most species the gamic female is apterous, and the male winged. The aphid cycle is less sharply defined than that of rotifers, and sex is only loosely connected with mode of reproduction. Among cladocerans, in typical cases, any female after the one that hatches from the fertilized egg may be parthenogenetic or gamic

or both. If she is parthenogenetic, her offspring may be either male or female.

Trematodes furnish many examples of parasites that regularly alternate between definite hosts. The life history of the lung fluke, *Pargonimus ringeri*, is as follows:

Where found	Free	Water	Snail	Water	Crab or crayfish	Man
Stage.......	Egg	Miracidium	Sporocyst ×	Cercaria	Cyst	Fluke
Generation..	1	1	1	2	2	2

Many trematodes have a redia stage in the snail following the sporocyst.

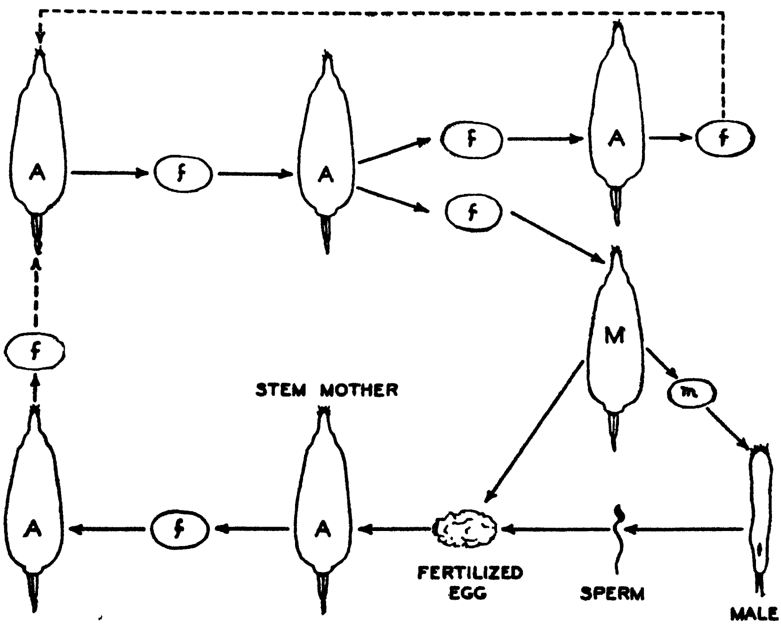


FIG. 125.—Alternation of amphigenetic and parthenogenetic generations in a rotifer, *Lecane inermis*. Generation *A* reproduces exclusively by diploid parthenogenesis, its eggs *f* invariably develop into females, and this type may continue for many generations. Some daughters *M* of parthenogenetic females may produce haploid eggs *m* which develop parthenogenetically into males or, if fertilized, produce parthenogenetic stem mothers *A*. (*After Miller* 1931.)

Other Types of Alternation of Generations.—It is possible that other types of alternation of generations besides metagenesis and heterogenesis occur. Among nematodes there have been

cases reported of alternation of hermaphroditic and dioecious generations, but none such has been proved. In certain pelagic ascidians belonging to the genus Salpa, life histories are very complex. The mother Salpa gives rise, by budding, to her sons; and each son serves first as a depository for one of his mother's unfertilized eggs, then as a living incubator within which his mother's daughter is housed and reared, and lastly as a father (Michael 1917). Among Salpas solitary and colonial, or "aggregate," generations alternate with more or less regularity, but they show great complications of a metagenetic cycle.

Functions of Alternations of Generations.—Alternation of generations shows more or less correlation with environmental conditions. This is true to a greater degree of heterogenesis than of metagenesis. Hydroids pass through their metagenetic cycle as fast as the environment permits without particular regard to its conditions, except as they limit metabolic processes. Metagenesis is generally an alternation between stages that occur where an abundant food supply is available, which permits rapid multiplication by budding, and stages that are concerned with sexual reproduction and distribution. Heterogenetic life cycles usually show parthenogenetic phases when conditions (temperature, food, etc.) are favorable for rapid production of individuals, and sexual phases when conditions of existence become more severe (winter, drought, etc.). In both types of alternation of generations rapid multiplication, when it occurs, usually takes place when conditions are stable and food is abundant; fertilization stages are more often associated with changing environmental conditions, particularly when such changes make the environment unfavorable for continued activity.

CHAPTER XIII

INTERSPECIFIC RELATIONS

Kinds of Associations between Different Types of Animals.—Animals of different species have varying degrees of intimacy in relations to each other, from complete indifference to such close connections as those of parasitism and symbiosis. For example, Nutting (1914) describes the animals associated with alcyonarian corals as: (1) harmless species, such as certain ophiuroids and molluscs, which do not modify the structure of the corals; (2) annelids, barnacles, crabs, and shrimps, which become overgrown more or less and thus modify the structure of the corals but do not subsist on their tissues; (3) true parasites (crustaceans, clams, annelids), which subsist wholly or in part on the corals; and (4) millepores and colonial anemones, which do not take away food but destroy corals by growing over and smothering them. Wheeler (1923) states that myrmecophiles and termitophiles may be classified as "predators, indifferently tolerated guests, true guests, and parasites."

Wheeler describes a peculiar coenobiotic association which he found in Arizona. Five or six organisms cooperate to form this. The oak, common in the Huachuca Mountains, was heavily infested with mistletoe. Larvae of a beetle made borings in this, and these were tenanted by colonies of the ant *Cremastogaster arizonensis*. On the inside of the ant galleries were numerous scale insects, later described by Cockerell as *Pseudococcus phoranderi*, which slowly kill the mistletoe. Thus the ant, which fosters the scales injurious to the mistletoe, which is a serious parasite on the live oaks and other trees, may be regarded as a useful forest insect (Mann 1913).

Caullery (1922) says:

Commensalisme, parasitisme, symbiose sont des catégories de notre esprit, qui ne sont séparées dans la nature par aucune discontinuité et qui offrent des aspects diverses des mêmes lois générales.

Degree of Association between Different Species.—Calvert (1922) and others have made formulae for computing the degree

of association that different species of animals show to each other by using as a basis correlation in distribution. Forbes and Richardson (1908) in discussing fishes say that there is a

. . . frequency tendency of closely allied species inhabiting the same territory to avoid each other's company, thus to evade competition with one another, by the choice of habitation. In consequence of this tendency, we sometimes find widely unlike species more closely and commonly associated in our collections than like, the ecological repulsion of each for its similars bringing dissimilars together in more or less definite associate groups.

In some cases different species are commonly associated because they seek the same habitat, and in others one or both of the associates seeks specifically for association with the other. Hindel (1905) found 32 species of insects in the willowcone gall: 1 gall maker, 10 inquilines, 16 parasites and hyperparasites, and 5 transient or accidental guests. In this instance the gall maker, guests, and inquilines seek a particular habitat in a more general way than the parasites, which depend on special hosts. The spiders that mimic driver ants and accompany them during their travels show a highly specialized relation to another species. Thus animals may commonly associate with each other for rather general, or even accidental, reasons or for very special reasons. Among ants and termites there are various relations. "The chief enemies of ants are other ants, the fiercest and most implacable enemies of termites are not other termites, but ants." Wheeler (1936) describes five types of associations: (1) ants that as hostile raiders raid, capture, devour, and enslave other species of ants and termites; (2) robber ants which "wrest termite prey from raiders"; (3) minute thief ants which prey on termite brood or disabled individuals; (4) inquilines which "inhabit portions of termitaries as indifferent neighbors"; and (5) guest ants which live among termites on a friendly footing, like members of a mixed colony of ants.

Predator and Prey.—Perhaps the relation between predator and prey is the one most generally present between animals of different species. One of the chief means that man has for combating pests is through the introduction or fostering of natural enemies. Much has been written in this field. For example, Davis (1919) has discussed the relations of the phyllophagous

beetles in great detail and gives elaborate diagrams showing relationships to various enemies. He states that the increase of the white grub in many localities has been due to the destruction of enemies (skunk, etc.) that formerly kept it in check. He also points out that the duration of various stages in the life cycle of a June beetle is definitely related to the number of enemies that usually attack it. The egg and pupal stages are short, well protected, and preyed upon by very few animals. Vine (1896) published a list of predaceous and parasitic enemies of aphids. Sladen (1912) did the same for bumblebees; and Wall (1906) for snakes. Folsom (1923) gives lists of animals attacked by various predaceous insects, and Ferton (1910) made similar studies of hymenopterous insects. Hudson (1922) mentions a certain year on the pampas when mice became extraordinarily abundant and ate up nearly all the bumblebees. In turn, the mice were beset by a host of enemies; owls appeared in great numbers, and other predators were abundant. It is usually thus—predators increase and decrease with their prey. Small animals, like insects, are influenced by temperature and humidity (Ball, Reeves, Boyden & Stone 1935, Thiem 1933); larger animals, such as grouse, depend more on food and adequate shelter (Bump 1933); and predatory animals may greatly decrease the numbers of food animals (Berndt 1933, Brower 1934). Raptores in general eat types of food birds that are most abundant and easily available (Tinbergen 1932, Uttendorfer 1932). Predators maintain a balance in any biome. The destruction of one species may disturb this and bring trouble to man by allowing undestroyed species to increase so that they become pests (Dice 1925). Forbes (1880) has discussed the interactions of animals in a very thorough manner, particularly the numerical relations between prey and predator.

It is a general law that vegetarian or scavenger animals are more numerous than predaceous species. There must be enough of the species preyed upon to supply the predators without being exterminated. Hingston (1920) noted that predatory ants in the Himalayas were not only fewer in numbers than the harvesters on which they preyed but differed from them in their greater swiftness and activity and in their habits of not following regular trails. Many animals have their scheme of life related primarily to escaping from enemies, and others spend their

existence continually seeking for other species that they may devour. A walking stick remains immobile for hours at a time and when it moves goes with great slowness in order that its resemblance to a twig may not be negated. Among the little bees of the genus Halictus, the male and female take turns standing guard at the entrance of their burrow in order to keep out their arch enemies, the mutillids, and other predatory insects that attempt to invade their homes (Melander & Brues 1903). The habits of termites in avoiding light and always building hard-walled, covered roadways for their necessary travels generally protect them from predaceous ants and other enemies.



FIG. 126.—Goosefish, *Lophius piscatorius*, preparing to gulp down a herring gull which is asleep on the surface of the ocean. (*After Gudger* 1929.)

All sorts of relations exist between predatory animals and their prey. There are many coelenterates which catch and eat fishes (Gudger 1934); and there are fishes that not only lurk among and gain protection from the stinging tentacles of Physalia but also devour the tentacles and polyps of their host (Kato 1933). The larvae, and even the adults, of some lepidopterous insects are predaceous (Balduf 1931). Anglers lurk on shallow bottoms and gulp in unwary fishes and birds that pass near them (Fig. 126; Gudger 1929*a*). Spiders commonly spin characteristic snares to capture prey. There is one species that spins a few inches of silken thread which has a sticky globule at its distal end. When an insect approaches, the spider whirls the thread about and attempts thus to ensnare it (Hacker 1935).

Robbers.—Some animals do not prey upon others directly but rob food-laden individuals. Forbes (1885) tells how frigate birds lurk in the lee of islands, whence they may pursue gorged noddy terns and compel them to regurgitate partly digested fish, which they skillfully catch in the air before it reaches the surface of the ocean. According to Hall (1900), the great skua gull has similar habits. Bald eagles commonly chase ospreys and rob them of their prey. Gudger (1929*b*) has given an entertaining account of how laughing gulls steal fishes from pelicans (Fig. 127). Wheeler (1911) describes flies that stand beside the trails of

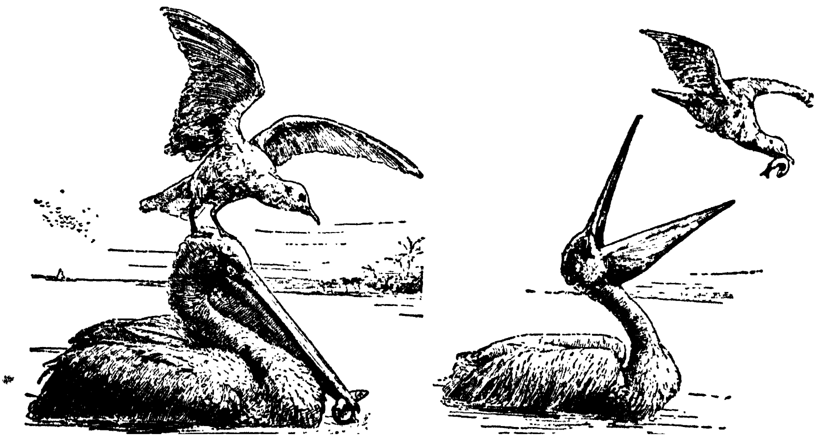


Fig. 127.—Laughing gull observes a pelican catching a fish, alights on its head, and, when the pelican raises its beak to swallow its catch, snatches the fish and flies away. (*After Holder, from Gudger* 1929*b*.)

foraging ants and capture food from the individuals returning to their nests. In Nigeria the writer observed flies (Bengalia) that preyed upon ants that robbed termits' nests. A fly would station itself beside the partly roofed-over trail of the rushing caravan of laden ants. Suddenly it would dart into the files, snatch up an ant, and cast it on the ground. The ant then dropped its termite, which was quickly appropriated and eaten by the fly.

Protection from Predators.—Animals that are preyed upon have developed various means for escaping from enemies. Inherent anatomical and physiological adaptations provide for the safe operation of living organisms when they fit their environments (Meltzer 1907). To meet dangers from predators animals

have spiny skins, repugnatorial glands, stings, and other distasteful qualities (Fig. 128). Coelenterates commonly have nematocysts which sting and poison food or enemies. These little stinging capsules are devoured by nudibranch molluscs and turbellarians and serve to some degree to protect their new owners. Warning colors serve to give notice to discriminating predators that animals are undesirable (Cott 1936). Some animals practice autotomy. Parts are cast off and left in the possession of the predator while the prey escapes. In Colombia there is an earthworm that is commonly found under logs.



FIG. 128.—A hedgehog, when it falls into the hands of an enemy, folds its nose and legs against its stomach and draws a muscular puckering string. Thus it stretches its skin so as to enclose its body completely in a mass of erect spines. Nigeria.

When exposed, it breaks in two; the posterior end wiggles vigorously while the anterior end quietly sneaks away. Ophiuroids, crustaceans (Wood 1932), lizards, and rodents (Sumner 1918) commonly shed their arms, legs, or tails when grasped.

Types of Associations between Animals of Different Species.—It is chiefly the activities of the predator seeking food and the reaction of the prey to avoid being eaten that have led to the intimate associations between animals of different species, but a few associations have apparently come about through the seeking of shelter, transportation, or other desiderata. It is difficult to classify the interspecific relations into groups because they constitute a graded series. It is unfortunate also that different usages obtain among botanists and zoologists in regard

to the terms connected with such associations. Coulter, Barnes, and Cowles (1911) use "symbiosis" to include all intimate interspecific relations, making "commensalism" and "parasitism" subdivisions under it. Zoologists have generally used these three terms as follows:

Commensalism. An intimate association between two or more species, in which one or more may be benefited but none is injured.

Symbiosis or *mutualism.* An intimate association between two or more species which results beneficially to all concerned.

Parasitism. An intimate association between two or more species in which one (host) is injured and the others (parasites) benefit.

In many cases it is not possible to say whether certain animals are related to others as commensals, symbionts, or parasites. This is often on account of lack of knowledge. Wallin (1923) has proposed the term "prototaxis" to include all cases where there is an "innate tendency to react in a definite manner to another organism." He would include conjugants, symplasms, symbionts, parasites, etc. As it is often impossible to say whether animals found associated with hosts are commensals, symbionts, or parasites, a general term is needed which will include all types of associations, whether injurious, beneficial, or neutral. The writer has therefore (1939) suggested the use of the word *consors* (pl., *consortes*). For example, when a worm is regularly found associated with a particular host it may be called a consors if one does not know what its relations to its host may be.

COMMENSALS

Commensalism.—The term commensal was originally used by Van Beneden (1876) in referring to animals that share the same food[1] but has now generally come to have a broader meaning and includes all intimate associations between different species of animals that are not parasitic or symbiotic. Commensals are associated, and, though one may derive more or less benefit, the other member of the partnership is not essentially injured or benefited. Van Beneden looked upon commensalism as hospitality in which a large or successful species helped, or tolerated the presence of, another species without any particular sacrifice.

[1] "Le commensal est simplement un compagnon de table."

"The messmate does not live at the expense of his host; all that he desires is a home or his friends' superfluities." Barnacles are commonly attached to whales, and some species are not found elsewhere. Most of these are commensals, but some of the more specialized species work injury by causing sores in the skin and hence are parasites. The great nests of the wood rat, *Neotomoma fuscipes macrotis*, harbor many animals. Davis (1934) classifies the insects in them as (1) seasonal inhabitants, such as dormant tenebrionids and coccinelids; (2) those brought in with building materials (Ptinidae, etc.); (3) incidental insects which feed on other insects, feces, fungus, etc.; (4) insects peculiar to rat nests and feeding on nest materials (commensals) or the rats themselves (parasites). Insects collected included Thysanura, Collembola, Orthoptera, Corrodentia, Anoplura, Hemiptera, Dermaptera, Coleoptera, Lepidoptera, Diptera, Siphonaptera, and Hymenoptera as well as Araneida, Diplopoda, and Chilopoda. Most of these animals were accidental residents which might have lived as well elsewhere, but a few were established commensals in rat nests.

Relations between Commensals and Hosts.—Commensal relations are not always concerned with food but may relate to shelter, migration, or other things. Sometimes they are temporary. Longley (1918) says:

> Fishes of different species may establish relations with one another which persist for days. Of such partnerships one of the most interesting I observed was between a red goatfish and a small yellowtail which I saw a number of times hunting for food together.

The larger fish stirred up the mud and its companion watched near by to snatch any small animals that escaped. Hecht (1918) tells of another type of temporary association. In this case a young amphipod (Orchestia) lived in the oral siphon of an ascidian, where it obtained food from the current but if disturbed swam freely and left its temporary host. Essenberg (1918) states that the distribution of certain polynoids is limited by the distribution of the animals with which they live commensally.

> The perfect color mimicry of commensal polynoids suggests that there is some chemical or enzymatic interaction between the messmates and the commensal, producing similar color patterns in animals widely different in kind.

Clark (1921) also noted that many small commensal animals were colored like their hosts, and he found that a crustacean (Alpheus) removed from a crinoid soon returned. He believes that symbiosis and parasitism have their origin in commensal relations. There has been no uniformity of usage in regard to the terms "commensal," "guest," and "messmate." To the writer it seems proper to refer to all animals that have intimate relations, from which they may derive more or less benefit, with animals of other species as commensals. It also seems proper to refer to those species which give support or shelter to commensals as "hosts."



FIG. 129.—Commensal worms (Spirorbis) growing inside the lip of a shell (Polineces) occupied by a hermit crab, Massachusetts.

Commensals That Live near Hosts.—In South Africa a weaver bird, *Hyphantormis capensis*, builds its nests in close proximity to the nests of a buzzard, *Pterolestes rufofuscus*. It thus escapes danger from such enemies as snakes and rats (Joubers 1932). The falcon, *Falco peregrinus*, lives largely on waterfowl and captures its prey only during flight. Certain ducks and other birds which nest on the tundra congregate near the eyries of the falcons and escape capture by not flying there; they walk to and from their nests, often for long distances. The falcon keeps other predatory animals (such as foxes, sea eagles, and gulls) away from the vicinity of its own nest, and other birds take advantage of this safe area (Buturlin 1933).

Commensals Attached to Outsides of Hosts.—Many commensals are simply fastened to the outsides of their hosts. They thus

gain attachment, perhaps some protection from the relation of the host toward certain enemies, and when the host moves are carried to situations favorable for respiration, the finding of food, etc. Vorticellids ride about on hydras, planarians, leeches, snails, insects, fishes, and salamanders; some species are associated with particular hosts because they require particular types of surfaces for attachment (Faure-Fremiet 1906). The remora attaches its sucker to a shark. The shells of hermit crabs may bear actinians, hydroids, bryozoans, worms, snails, and other animals. Wheeler (1911) says:

> Kneissl describes a mite that is attached to an ant's tibia by an anal secretion. It is licked and fed by ants and has an adaptation for turning from side to side while being licked without losing its hold.

A large clam (*Atrina rigida*) cast up on a Florida beach had more than 100 animals of 25 species attached to it (Perry 1936).

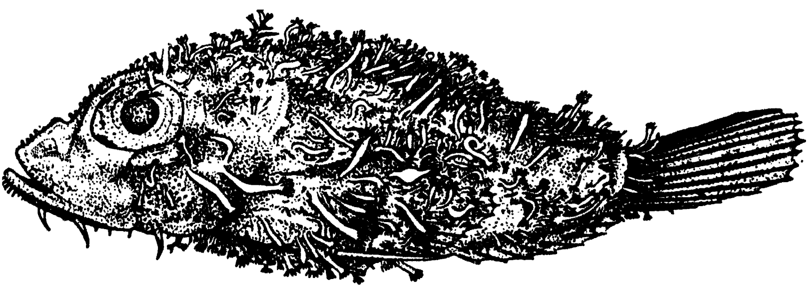


FIG. 130.—Hydroids, *Podocorella minoi*, growing on a scorpaenoid fish. (*From Komai* 1932*a*.)

Little crabs cling to the spines of sea urchins and thus gain protection (Parker 1936). Hydroids like Hydractinia are commonly associated with hermit crabs but also live in other situations where there are strong currents (Schijfsma 1935). Many of the animals associated with hermit crabs (Fig. 129) probably profit more by the currents produced by the crab than by the food left over from the crabs meals. Many sessile animals accidentally become attached to other living animals that have suitable exteriors; others are regularly associated with such hosts, and some cannot live without them. An animal that is attached to the outside of a favorable host may easily go further and take up symbiotic or parasitic relations.

Commensals within the Bodies or Homes of Hosts.—For commensals that invade the bodies or homes of their hosts, the development of intimate associations is perhaps much easier than among those which maintain relations from the exterior. When the Cossus beetle makes borings in tree trunks, other insects are attracted by the sap and the shelter (Joy 1914). Dollman (1910) has reported 10 species of beetles that live in moles' nests. Ainslie (1906) found the larvae of flies (Drosophila) regularly living in the spittle masses of cercopids. In the burrows of moles and rodents a variety of insects and other animals regularly live (Davis 1934*a*, Dollman 1910, Wlassow 1933). Crab holes and crayfish burrows may give shelter to numerous animals (Creaser 1931). Often there are three or four grackles' nests tucked away among the sticks of an osprey's nest (Bahr 1907). Certain gall flies, mosquitoes, and midges habitually nest on spiders' webs (Knab 1912). The tubes of worms and other burrowing animals often contain commensals (Fig. 131). Sponges are often veritable living hotels. In one loggerhead sponge, *Speciospongia vespara*, at Dry Tortugas the writer (1932*d*) counted 17,128 animals which belonged to 10 species. Snails, worms, and other animals live inside the shells of hermit crabs (Fig. 129). Fishes that live among the tentacles of actinians or corals, or actually within the bodies of their hosts, gain the protection afforded by nettling cells. The crustaceans that live within medusae get similar benefits and transportation as well. There are many instances of animals that live within others: crabs dwell in molluscs; fishes and prawns in sea cucumbers; shrimps, in actinians, sponges, salpas, ctenophores; etc. Cushman (1919) has described a foraminiferan that lives within the shell of another, which assumes a peculiar form as a result.

Commensals in Colonies and Societies.—When groups of animals occur it is often easy for commensals to find shelter among them. Animals live in bryozoan (Souche 1935) and coral colonies, where they are often invested with gall-like growths. Flies live as tolerated guests in wasps' nests (Nixon 1934). There are many species of termitophiles and myrmecophiles (Emerson 1935, Wheeler 1926). These include beetles, aphids, ants, millipedes, isopods, etc. A number of larval insects are found in the nests of bumblebees; some of these are accidental guests, and some are parasites that have hard or spiny coverings

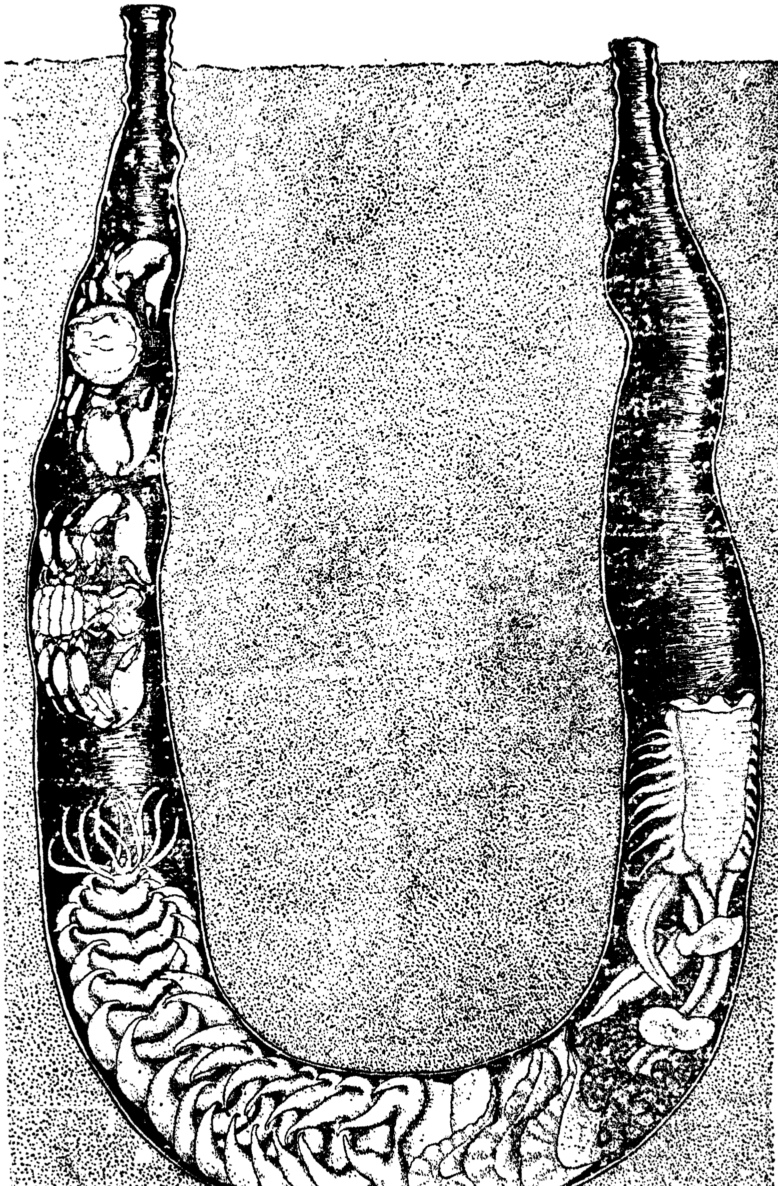


FIG. 131.—Section of a worm tube (Chaetopterus) buried in sand. A pair of commensal porcellanid crustaceans (Polyonyx) live in the tube with the worm. (*From Pearse* 1913.)

for protection (Sladen 1912). The driver ants (Dorylinae) are accompanied on their travels by many myrmecophiles. Wasmann (1914) groups these camp followers under three heads: (1) symphiles, which are agreeable to the ants on account of exudations that they give off; (2) mimics, which often show remarkably close resemblances to their hosts; and (3) various animals that are protected by hard shells and are often greatly flattened.

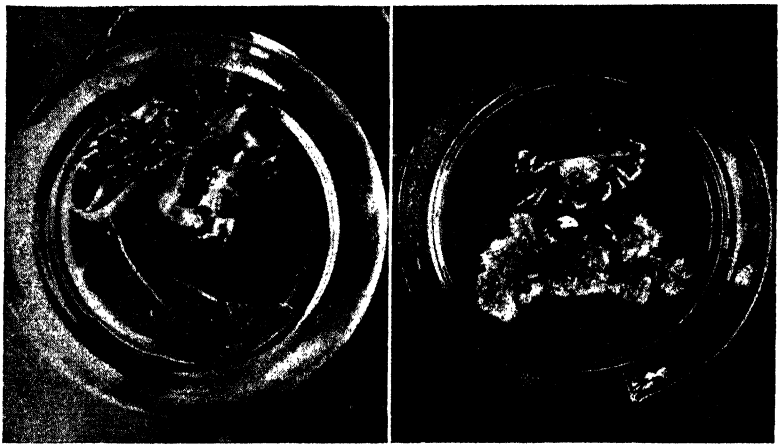


FIG. 132.—Commensal crustaceans from a Chaetopterus tube. Those on the left are porcellanids (Polyonyx); those on the right are crabs (Pinnixa). The Pinnixa above has just shed its shell and is quite clean, but the one below is covered with a growth of bryozoans, which are commensals on a commensal. (*From Pearse* 1913.)

Often commensals are attended to by their hosts; in other cases they remain unnoticed. Wheeler (1911) says:

Crawley made several observations on the relations of the little isopod, *Platyarthrus hoffmanseggi*, to various ants. He found that many species are hostile and devour or drive away these crustaceans, but that *Lazius flavus* and *L. niger* seem to be very tolerant of them. As a rule, *L. flavus* receives *Platyarthri* from the nests of its own species and others without taking notice of them. These small, blind woodlice pass their whole existence in ants' nests, and when they are about to molt or produce offspring, are found in small cells of earth made in the walls of the nest, where they remain for some time, finally breaking their way out. Apparently, the cells are made by the ants, since these insects were seen carefully plastering earth around the crustaceans. . . . The pseudoscorpion (*Chernes scorpioides*), found literally in thousands in *F. rufa* nests in Leichestershire, is treated with indifference by the ants.

Animals in Pitcher Plants.—Not only are animals inhabited by commensals, but pitcher plants, bromeliads, and other plants are often occupied by characteristic animal commensals. In American pitcher plants are found protozoans, mosquitoes, wasps, moths, tree frogs, etc. In Java and Sumatra Thienemann (1932) recorded in pitchers (Nepenthes) the following numbers of species of animals: 7 Culicidae, 1 Chironomidae, 1 Cecedomyidae, 1 Syrphidae, 7 Phoridae, 1 Lepidoptera, 2 Chalcidae, 2 Araneae, 6 Acarina, 3 Harpacticidae, and 3 Rotifera.

SYMBIONTS

Symbiosis.—Symbionts are animals, or plants and animals, of different species that live together to the mutual advantage of each (Yonge 1935). It must be remembered, however, that some botanists use the term "symbiosis" in a different sense. McDougall (1918), for example, argues that it is a mistake to apply symbiosis to "a few cases of reciprocal parasitism," when De Bary (who first used the term) intended it to have a much broader meaning. Yet Nuttall (1923), who gives a comprehensive review of intimate relations between plants and animals, says:

> The term symbiosis denotes a condition of conjoint life existing between different organisms that in a varying degree are benefited by the partnership.

The nature of symbiotic relations varies considerably. It may be concerned primarily with food, protection, and other essentials, or even luxuries, of life. In some cases symbionts come together more or less by accident; in others one member of the pair may seek actively and care for the other. Many symbionts have special adaptations which distinguish them from other animals of the same type. McIndoo (Weese 1921) has described extravagantly developed glandular knobs on the abdomens of certain staphylinid beetles that live in termites' nests in British Guiana. These give off secretions that make the beetles much sought after by the termites, which continually lick them. Many of the examples that have been cited as symbiotic will probably not stand up under careful scrutiny. A number have already been shown to be cases of commensalism or parasitism. The real question in any particular case is whether *both* species

in the partnership are *benefited*. It is often not possible to come to a definite conclusion.

Wheeler (1923) says:

> Social life may, indeed, be regarded as a special form of symbiosis. This term, which signifies the living together of organisms in a balanced, cooperative, reciprocally helpful manner, is commonly applied inter-specifically, that is, to partners thus related belonging to different species, but there is no reason why it should not be applied to the same kind of relations between individuals of the same species, that is, intraspecifically.

Wheeler also points out that probably few animals attain to a perfectly symbiotic relation and that symbiosis often lapses into parasitism. Van Beneden (1876) says:

> When a copepod crustacean installs himself in the pantry of an ascidian, and filches from him some dainty morsel, as it passes by; when a benevolent animal renders some such service to his neighbor, either by keeping his rack clean, or removing detritus which clogs certain organs, this crustacean or this animal is no more a parasite than is he who cowers by the side of a vigilant and skilful neighbor, quietly takes his siesta, and is contented with the fragments which fall from the jaws of his companion.

Crustaceans and Coelenterates.—The examples of symbiosis that are best and most widely known are perhaps those between crustaceans and coelenterates. Thomson (1923) tells of a small spider crab that made its home beneath the spreading tentacles of an anemone. When the crab went out foraging and brought back food, the anemone took it away, and the crab appeared to satisfy its hunger largely from the undigested fragments that the anemone discarded. Balss (1924) has made an extensive review of the symbiotic relations of hermit crabs with other animals. He lists 20 species of actinians that are more or less regularly associated with 25 species of hermits; 8 hydroids on 12 hermits; sponges, bryozoans, and annelids. Some of the hermits, when changing to new shells, are known to transfer their symbiotic anemones to their new dwellings. If deprived of their anemones some hermits will search tirelessly until they find new individuals for their shells. Some of the hermits do not take food directly but wait until it has been stung by the nematocysts of their attached coelenterates. Certain little crabs (Melia) carry

anemones in their claws and use them in securing food and for defense. If threatened they hold the anemones out toward the enemy. Duerdin (1906) studied the behavior of Melias. He states that several species of actinians are used by the crabs and that if a whole one cannot be obtained a piece is held. The chelipeds are not used for feeding, but the actinian secures the food, and the crab then takes it away. He says that the actinians can exist indefinitely without the crabs but that the crabs must have actinians. On the coast of Japan there are actinians and hydroids that are commonly attached to certain fishes.

Vermin Removers.—Some small animals often associate with larger species, keeping them free from vermin and in some cases giving them notice of danger. Longley (1922) observed a small fish of this sort at Tortugas:

> *Thalassoma nitidus* is commonly seen pecking at the surface of larger fishes, presumably cleaning ectoparasites from them. These larger fishes return again and again to submit to the process of grooming and will drive away others which interrupt the process. . . . Attentions are not merely tolerated but actually welcomed.

The imouran, a large rodent in Mongolia, is said by Ossendowski (1922) to be attended by a lark which perches on its back, picks off parasites, flies above its host, and utters cries to give notice of danger. A plover is said to pick the teeth of crocodiles (Van Beneden 1876). Certain birds sit on the backs of buffaloes, cattle, rhinoceroses, and other animals. They eat bloodsucking insects and parasites and give warning when danger threatens.

Hymenopteran and Termite Symbionts.—Ants and termites have symbiotic relations with a considerable variety of animals and plants. Mann (1913) describes a butterfly in Java that deposits eggs on an ant plant. The caterpillars that hatch are commonly attended by ants, and those that do not receive such attention die. The former give the ants a sweet secretion and are fed in return. Another caterpillar that is attended by ants displays repellant organs when it has no desirable secretions ready to be licked off by the ants. Many species of birds nest in association with wasps, ants, and termites and give mutual protection (Myers 1935). There are mites that live in pouches in certain bees and keep the backs of their hosts free from excess pollen (Leveque 1932). Ants care for and receive food from aphids, membracids, and scale insects (Andrews 1930).

Plants and Animals.—A number of plants are symbiontic with animals. Certain termites and ants raise fungi for food, and some of the plants that they thus utilize are not found outside their nests. Other algae and fungi live in the bodies of animals and help in the digestion or assimilation of food. Nuttall (1923) states that plants within animals assist animal metabolism or other processes in various ways, *i.e.*, decompose urates (Stammer 1935), produce enzymes that aid in sugar digestion (Heitz 1927), digest cellulose, fix free nitrogen, produce light, etc. Zooanthellae occur in protozoans, sponges, coelenterates, ctenophores, turbellarians, rotifers, annelids, bryozoans, and molluscs; and bacteroids in the intestines of cockroaches, beetles, flies, butterflies, and molluscs. Some of these may be slaves or parasites, but others appear undoubtedly to be symbionts (Caullery 1922, Welsh 1936). Certain species of termites are unable to digest wood unless they have symbiotic protozoans in their intestines (Cleveland 1923, 1924). Perhaps the most interesting of the symbiotic fungi are the mycetomes that live in the fat bodies of a number of insects, where they contribute to the insects' metabolic processes (Koch 1931). They give off minute spores which invade the eggs of the insects, and thus the symbionts are hereditary. The relations of flowers to animal pollination have already been discussed in Chapter XI. In Northern Africa certain flowers (*Ophrys* sp.) resemble female insects and are visited by males, which pollinate them (Faegri 1935).

Origin of Symbiosis.—Symbiosis appears in most cases to have had its origin in chance associations between animals of different species. Huxley (1912) says that scientists generally

> . . . now suppose that one organism does not merely rush into a ready-made vacuum provided by the other, but that the two should conspire together to create a vacuum of their own, into which, as fast as it is created, they jointly creep. This is, in effect, what happens when two species become mutually dependent.

Wheeler (1923) describes tachigalid beetles which live in hollow petioles. Aphids wander into their dwellings and become important contributors of food to the beetles. Aphids that give food to other insects when solicited escape being eaten on account of this habit, the sweet secretions being more acceptable than the body of the producer. Balss (1924) and Brunelli (1913) who

have made intensive studies of the relations between hermit crabs and their symbionts are convinced that symbiosis did not come about through modification of habits that certain crustaceans have of placing objects on their backs but arose through accidental contacts and perhaps in some cases through the activities of the crabs. Anemones, hydroids, sponges, and other animals associated with hermits are commonly found attached to shells and other objects, which do not contain hermits. Kropotkin (1916) Framintzin (1907), Caullery (1922), and Wallin (1923) have stressed the importance of symbiosis as a factor in evolution, claiming that it has been important in enabling animals to attain higher levels.

Effectiveness of Symbiotic Relations.—There can be no doubt that symbiosis is useful to many animals. Balss (1924) has shown that hermit crabs that carry anemones get the benefit of the nematocysts (which sting enemies and kill prey) and protection of the shell from gradual wear and injury. In some cases the actinian takes the place of a shell and completely covers the hermit's soft abdomen. The anemones are transported from place to place, are likely to secure food because the crab continually seeks it, and are rather certain to be kept in pure, well-aerated water.

Goto (1910) describes two species of hydroids that live along the Japanese coast that

> . . . have the same habit of living always in symbiosis with a hermit crab, *Eupagurus constans* Stimpson, and of forming shells of their own composed of a chitinous framework, so that in most specimens there is apparent no basis of gasteropod shell, as in the case of most known species of Hydractinia.

Polimanti (1911) studied the relations between a sponge and a crab and concluded that

> It is certain that the crab takes the initiative in putting the sponge on its cephalothorax. It is also certain that the sponge affords the crab a genuine protection against the appetite of cuttlefishes.

In cases like that described by Durden (1906) there seems to be no doubt that an anemone is transported to food and that its transporter depends on the anemone to secure its food. Aphids furnish food for ants and are, in turn, fed and protected. The

eggs of certain species winter in the underground galleries; the young aphids are carried out by the ants in spring and placed on favorable food plants. Aphids supply honeydew to ants, moths, flies, and beetles but are cared for only by ants (Ord 1910). The protozoans in termites and ruminants appear to be essential for the digestive processes of their hosts and receive food and protection. The rhinoceros, by tolerating its attendant bird, is freed from ticks and warned of danger. On the Siberian steppes is a bird (*Oenanthe isabellina*) that build its nests in the burrows of a ground squirrel, *Citellus eversmanni.* It warns its host of danger by a characteristic cry (Zverev 1927).

Reinheimer (1921) has discussed the relations of symbiosis to food. He believes that symbiosis arises when there are "a pair of opposites to be accommodated," each having something the other needs. "The presence of symbiotic systems makes on the whole for increased economy and increased security of life." Reinheimer argues for the importance of "cross-feeding" as opposed to "in-feeding" and says: "Surely the chances of fruitful, social, and mental life are therefore higher among cross-feeders than in-feeders."

PARASITES

Parasitism is an intimate relation between two animals in which one is injured. Usually the parasite takes food from its host, but parasitism is not always concerned with food relations. Parasites may do injury by occupying space within the bodies or dwellings of their hosts, by giving off poisons, and by other means. Parasites are scattered throughout the animal kingdom and, though they are most often found among protozoans, platyhelminths, nematoids, and arthropods, most other phyla have species that have taken up life as parasites.

Types of Parasites.—Ectoparasites live on the outside of their hosts, and endoparasites live within; but there is no sharp line of demarcation, and some species may either live on the outside or invade the interior, occupying such spaces as are furnished by buccal or branchial cavities. Some species of animals that are parasitic need not lead such a life and hence are known as facultative parasites. On the other hand, obligate parasites cannot exist except in close association with their usual hosts. Some parasites (permanent) must be continually associated with their

hosts; others (transitory) may come in contact with their hosts only at intervals or during certain stages in their life histories. Social parasites invade societies and gain a living at the expense of the community. Accidental parasites are animals that would not usually lead such a life but through some unusual circumstances have become associated with hosts. Many parasites have attained a high degree of specialization in their host requirements. Some can live in only a single species of host; some require two or more specific hosts in order to complete their life cycle, and there is thus a regular alternation of generations and hosts. Parasites that have a simple life history and may have all stages associated with a single host are monogenetic, but those that have an alternation of generations and have relations with two or more hosts are digenetic or trigenetic. In the latter cases the primary, or definitive, host is that in which the adult or sexually mature phase of the parasite is found; and the secondary, or intermediate, host is that which contains the immature, parthenogenetic or asexual phases.

Examples of Parasitism.—An endless array of parasitic relations might be presented, and the following are selected as examples of rather diverse types. Synalpheus and Typton are two shrimplike crustaceans which live in the canals of the gigantic loggerhead sponge and, though belonging to different families, resemble each other closely in form and coloration. They eat from the walls of the canals in which they live, scraping off sponge tissues and accumulated materials (McClendon 1910). When two individuals meet they snap their claws at each other, and one or both back away. Claasen (Weese 1921) has described a midge larva that lives in swift streams, where it lurks under the wing pads of May-fly nymphs and sucks nourishment from the bodies of its hosts. Certain parasites are associated with crinoids, stealing from the food grooves and in some cases causing galls (Clark 1921). Calman (1911) says:

> The order Isopoda includes a very large number of parasitic species. The extensive family Cymothoidae presents a whole series of gradations in habits and structure between actively swimming predatory species and others which in the adult stage are permanently fixed to their host, usually a fish, and are incapable of movement. . . . No group of Crustacea exhibits more numerous examples of parasitism than the Copepoda. Every grade of transition between a free predatory habit

of life and the most complete dependence upon a host may be traced in various families of the subclass.

A hookworm bleeds its host by sucking blood and passing undigested droplets out through its anus. It also does injury by producing toxins which are absorbed by the host. A filarial worm (*Wuchereria bancrofti*) that lives in man produces hundreds of thousands of larvae in its host's blood. These larvae do little or no damage in man, and a few of them are sucked out by mosquitoes and injected into new hosts. The adult filarial worms occlude lymph glands and may thus cause elephantiasis.

Social Parasites.—Colonies or societies are often preyed upon by animals of other species. Though certain young fishes live among the trailing tentacles of pelagic coelenterates for protection, some fishes also feed on the tentacles (Scheuring 1915). In Brazil there is an amphisbaenian which lives in the nests of leaf-cutter ants and eats its hosts (Bates 1892). Certain coccinelids live in ants' nests and prey on coccids that ants bring in (Wheeler 1911). Phorid flies wait persistently at the entrances of the nests of burrowing bees (Halictus) for a moment when the doorkeeper leaves the way open so that it may dart in and lay eggs on the stored pollen mass of its host. When a laden bee returns to a nest, a fly may succeed in laying an egg on its load of pollen before it enters. Halictids are also robbed by little ant thieves which burrow through the walls of their tunnels (Melander & Brues 1903). Parasitic bees (Psithyrus) live in the nests of bumblebees (Sladen 1912). Each species is quite specific in its choice of hosts and usually associates with a single species. A female enters a colony, stings the queen to death, and takes her place. She has a thick, hard exoskeleton which makes it difficult to injure her. There is a general tendency toward parasitism among bumblebees (Bombus); the queens of certain species often invade the nests of others. Wheeler (1923) described seven types of association of parasites with ants: (1) brigandage, by animals that snatch food from its rightful owners; (2) thievery, by small animals that live in the walls of nests and prey on the food stores or brood; (3) slavery, in which one species captures the brood of another and rears workers which become a part of the colony into which they are brought; (4) temporary social parasitism, in which workers kill their own queen after a foreign

female has invaded their nest, and the new queen gradually establishes her own workers with the aid of the original society; (5) permanent social parasites, in which a foreign female enters a nest, kills the original queen, and produces no workers but rears females for other nests; (6) ectoparasites on individual ants; and (7) endoparasites in individual ants. Again Wheeler (1911*a*) described four types of queen ants that are unable to live without the aid of another species: (1) a queen enters a nest and kills the original queen, or the original workers do so, and her workers gradually replace those of the hosts; (2) a queen enters a society, and a group of workers of two species results; (3) amazons enter a society, kill the queen, and maintain a mixed colony by capturing new worker brood at intervals; (4) a small, feeble queen enters a society and is adopted in place of the original queen, which is usually killed, no new workers are produced, and the group gradually dies after rearing the foreign invaders.

Origin of Parasitism.—The origin of parasitic habits is often associated with prolonged inquiline life or with attempts to secure food for the individual immediately concerned or for its offspring (Smith 1934). Sarcophagid flies usually deposit their eggs in dead flesh but sometimes lay them in open sores, and their larvae invade living animals. Barnacles on account of their sessile mode of life show a certain degree of degeneracy compared to many other crustaceans; certain of them (Sacculina, etc.) have apparently, after developing habits of attachment to particular animals, become parasites and now regularly depend on the absorption of nourishment from their hosts for their existence. Clark (1921), after considering many parasites among fossil animals, concludes that the assumption of sessile life by a species is often the first step toward parasitism. He also believes that commensals have often become parasites. Bouvier (1922) has described an interesting series of habit relations among pompilid wasps. Some species hunt for prey and lay eggs on it; others lay eggs on spiders captured by wasps of other species; and others search over the ground for a covered nest, remove the owner's egg, deposit their own egg on the stored food, and fill the burrow again. Froggalt (1915) says that blowflies in Australia learned within 12 years to lay eggs in the soiled, damp wool of sheep. He believes that the habit arose after there was a great decrease in the amount of carrion (poisoned rabbits, etc.)

available and claims that the wool-blowing habit has constantly increased. Two species of flies at first took up the habit, and another adopted it later. Brues (1921) believes that many hymenopters learned to lay eggs on living hosts before they began to deposit eggs on dead animals. Haviland (1922) is of the opinion that parasitic habits among hymenopters commonly arose from former inquiline modes of life. In New Zealand the kea formerly subsisted largely on insect larvae, honey, fruits, berries, and roots but now has learned to feed on sheep (Marriner 1909). Certain individuals perch on living sheep, the largest and strongest usually being attacked; tear holes in the back of their victims; and devour the fat. Other keas flock to the feast. Marriner states that the rhinoceros bird in Africa, which used to confine its attentions to ticks, has now learned to feed on living mammals by pecking holes in them. Quite recently magpies in the western United States have been observed to attack sheep.

Ewing (1912) has given a very thorough and illuminating discussion of the development of parasitic habits in mites. He shows that parasitism has originated at least eleven times in different groups. Among zoophagous types, parasites came from lines that were predaceous feeders, scavengers, or suckers of plant juices. Ewing believes that the assumption of parasitism by mites has been easy because of food habits and minute size.

> Among our living forms we can today trace out all the stages of advancing parasitism, including the occasional or erratic parasitism, semiparasitism, facultative parasitism, even to the fixed and permanent type, and finally to endoparasitism.

Herrick (1909) has discussed the origin of parasitic habits in cuckoos, and remarks on the lack of such habits among the cuckoos of America, where the cowbirds are parasitic.

> Possibly a lack of attunement of the cyclical instincts occasionally seen in all birds, and rather more frequently in these cuckoos, may have been the starting point of the parasitic habit of *Cuculus*, *Canorus*, and related old-world genera.

Barrett (1910) believes that cuckoos, and other birds of similar habits, began to lay eggs in the nests of other species when their own nests were not ready and they were obliged to lay at once.

The cowbirds in America show various degrees of parasitism. Those of some species build a rude nest on top of the one they have appropriated; others never build a nest and commonly throw one or more of the eggs or young of their host out of the nest. Among certain raptorial birds several females lay eggs together in a single old nest, where all cannot brood. It is possible in such cases that brooding parasitism arose from nest parasitism (Makatsch 1934). Among parasitic cowbirds (Fig. 107) several females often lay in one host nest (Friedmann 1929). The cuckoo bees deposit their eggs in the nests of host bees where they are reared (Reinig 1935).

Wheeler (1923) has shown clearly that social life is favorable for the development of parasitism. Wasmann (1909, 1911) holds that interspecific parasitism among ants has usually come from previous habits of robbery and slavery, though he also recognizes development through temporary parasitism, guest relations, and sudden mutations. Wheeler (1923) points out that parasitic social wasps usually lay their eggs in the nests of closely related species. They have no worker caste but are apparently descended from forms that did. He believes that trophallaxis, or mutual feeding, is largely responsible for social parasitism among ants.

Conditions Favoring Parasitism.—There are many conditions that lead to or favor parasitism. The ideal host for a parasite is one that is tolerant and at the same time resistant. It should live and furnish nourishment or other necessary things but not interfere with the activities of its associate. Hosts usually have various means for preventing the entrance of or eliminating parasites. Furthermore, parasites compete among themselves, and the presence of one species may inhibit the entrance of another into the same host. A parasite encounters continual difficulties in finding, entering, and remaining in hosts and must often enter into competition after it has gained a foothold. There are also many conditions of environment that may help or hinder parasites. The writer (1924*a*) has been able to show that wide range, ability to invade a variety of habitats, varied food, association with vegetation, and residence in shallow water are generally associated with a greater degree of parasitic infection among freshwater fishes. Blanchard (1907) found that a marmot could not be inoculated with trypanosomes, spirochetes, or trichinae

when it was in a hibernating state. Ewing (1912) states that widely distributed species of mites are often bloodsuckers and thus are able to secure a large amount of food in a short time. He also says that wide distribution among mites is usually correlated with the presence of ambulatory legs, ovoviviparity and habits of laying eggs away from hosts, and considerable resistance to variations in temperature and moisture. Ewing also points out that restricting factors are endoparasitic habits, delicate and degenerate digestive organs, specialized adhering organs, inability to live away from a host on account of climate, inability to carry on locomotion when off a host, and adaptation to a solitary or monogamous host. Van Cleave (1921) shows that all of the four species of parasites that infest the American eel are acquired in freshwater; in the European eel, seven are acquired in freshwater, and two in the ocean. The parasitic fauna of salmon changes as the fishes migrate from fresh to salt water and back again (Dogiel & Petruschwsky 1935). Freshwater fishes in general have more parasites than marine fishes (Ward 1934). It has long been known that the incidence of malaria in any region depends on several factors, such as susceptible men and anopheline mosquitoes, high humidity, and temperature. The coincidence of the optima of these determines the prevalence of malaria (Bodenheimer 1933).

Antagonism between Parasites.—As has been suggested, the presence of certain parasites may prevent those of other species from infesting hosts. Wilson (1917) states that lernaepodid crustaceans and the glochidia of clams are, as a rule, mutually exclusive when occurring on fishes but that a light infestation with one parasite may not be sufficient to keep off the other. Plath (1922) tells of a parasitic bee that will not tolerate another individual of its own species in the same nest. Semper (1881) noted that a parasitic isopod in one branchial chamber of a shrimp prevented the entrance of a parasite of the same species on the opposite side.

Qualities of Hosts.—A host has certain qualities that make it desirable or undesirable for a parasite. Brues (1908) in discussing hymenopteran parasites says that a host should be large enough to furnish food but small enough to be completely consumed when the parasite is ready to pupate. A restricted habitat, such as that of a wood borer, usually limits the number of parasites

that attack the occupant. Some hosts have few parasites because they pass through a short period when they are subject to attack. Van Cleave (1918) states that the seasonal distribution of acanthocephalans depends on the extent of time necessary for the infestation of a host, length of time the larval parasite must spend in an intermediate host, and seasonal changes in food habits or migrations of final hosts. Hosts are necessary for associated parasites in various ways and at various times. The parasites of birds going north during their spring migration may be quite different from those of the same species when going south in the autumn. The European salmon sheds certain parasites when it goes into freshwater and ceases to eat. Some hymenopterous parasites destroy their hosts after they attain their growth; others destroy the larvae or food of their hosts; and others destroy only the reproductive individual in a colony. Leiby (1922) describes a chalcid that invades a caterpillar but allows the host to live as long as possible. It feeds first on its host's fat body, then on its blood, devours the muscles and other tissues, and finally pupates in the skin. Animals that have homes are more susceptible to infestation by parasites such as fleas, ticks, and bird lice than are those that wander about continually.

Food Relations of Parasites to Hosts.—When parasites depend on their hosts for food, it is, of course, desirable to have the host injured as little as possible during the life of the parasite. A parasite that kills its host before it has satisfied its own needs is in a sense maladjusted and is not well adapted in its host relations. Parasites have all sorts of food relations with their hosts. The crab (Pinnotheres) that lives in the oyster scrapes mucous strings from the edges of the gills of its host, thus not injuring the body of the oyster but continually stealing food. Graenicher (1905) described a parasite that enters the nests of bees and lays eggs. The egg is deposited earlier than that of the host; the larva grows faster, first devouring the food stores and later killing the larva of the host. Certain chalcids mate in the open but deposit their eggs in ants' nests (Wheeler, 1907). The larvae feed upon the bodies of ant pupae, which are not killed but modified so that they develop into peculiar, dwarfed forms. Haviland (1922) describes a hyperparasite that attacks a chalcid which is parasitic on aphids. This waits until its host is fully fed before depositing its egg, and its larva then feeds and pupates

within the aphid skin. Body lice must have a more or less continual supply of nourishment; some ticks can live without food for years. The metabolism of both these arthropods is adapted to a parasitic mode of life, yet how different are their relations to their essential foods. Parasitism may be defined as follows:

> The lower limit of parasitism is at the change from a food supply that is discontinuous in space and requires locomotion and sense organs to acquire, to one which is continuous in space and is ample for the individual. The upper limit of parasitism is the complete loss of locomotor organs, sense organs and even accessory organs that have to do with discontinuous food down to the simple absorption of liquid food through the body wall (Kennedy 1933).

Structural Modifications of Parasites.—Parasites perhaps furnish the most striking examples of adaptation to be found among animals. Their structures, physiological qualities, feeding habits, reproduction, and behavior are often specialized to a high degree to fit particular hosts. Ectoparasites are commonly flattened; their organs of locomotion are often degenerate, and organs of fixation are commonly well developed; digestive organs are adapted to continual feeding or have developed great storage capacity so that an animal may gorge itself and then go for a long time without food. There are, of course, many exceptions to such general statements. For example, fleas are compressed and are thus able to move about readily among the hairs of mammals; they also possess unusual ability for locomotion. Endoparasites are not so commonly flattened, and many have lost their symmetry of bodily form completely. In all parasites there is a tendency toward loss of organs of vision and often of other sense organs also. Endoparasites commonly show a tendency toward the loss of enteric organs and a high degree of specialization in structures and activities associated with reproduction. The trends of adaptation associated with parasitism are nicely illustrated in various groups of crustaceans. The free-living copepods, in general, resemble Cyclops in form. The ectoparasitic argulids have retained their ability to swim actively but are very flat and have appendages modified into adhesive disks and hooks for clinging to their hosts. The lernaepodids have commonly taken up life as parasites among the gill filaments of

fishes. They are thus protected by the opercula of their host and are surrounded more or less by the filaments. They show various degrees of lack of metamerism and definite form and in specialized species are shapeless sacs. Isopods show similar lines of specialization: the free-living species having natatory appendages, the ectoparasitic species having flattened bodies and appendages modified for clinging, the endoparasitic species in some cases being extremely degenerate—mere membranous

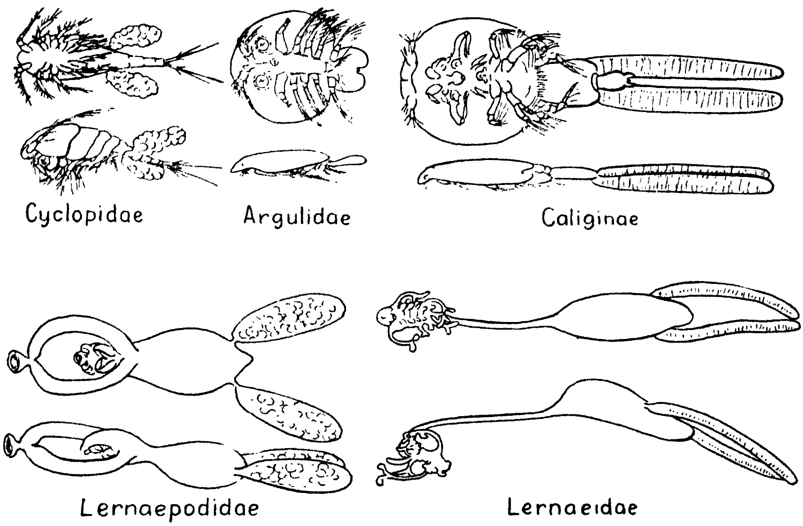


FIG. 133.—Free-living and parasitic copepods. Cyclopidae are free-living; Argulidae are swimming ectoparasites; Caliginae are feeble swimmers and rather sessile ectoparasites; Lernaepodidae and Lernaeidae are sessile parasites which have lost all swimming appendages. (*From Pearse* 1926*a*, *after Wilson.*)

sacs containing reproductive products (Caullery 1922). Among some crustaceans the effects of parasitism are the more apparent because only the females are parasitic and the males resemble nonparasitic representatives of the groups to which they belong (Van Beneden 1876). The same is true of certain mites (Ewing 1912).

Physiology of Parasites.—The physiology of external parasites often is not very different from that of comparable free-living animals, but the activities of endoparasites are adaptable to the peculiar conditions in which they live. Ectoparasites of homeothermic vertebrates are adapted to rather high temperatures. Such animals as mosquitoes, lice, and fleas often show strongly

positive reactions to warm objects. An endoparasite lives in the food or body fluid of its host. It must ingest or absorb food without being killed and digested. Calcareous bodies are often present in the bodies of such parasites. These may perhaps neutralize the host's enzymes and other substances that might injure a parasite. As parasites go deeper into the bodies of their hosts, they have increasingly unfavorable conditions for respiration. Copepods that live in internal cavities often have large gills. Many endoparasites have remarkable ability to live in media that contain little or no oxygen. They are adapted to special conditions which are more or less characteristic of each species of host.

Specificity of Parasites for Particular Hosts.—All through the animal kingdom there are trends toward dependence—toward a narrow environment (Huxley 1912). Among parasites this is often manifested by the remarkable degree of specificity shown in host relations. Though the glochidia of some species of fresh-water mussels occur on several species of fishes, a considerable number are confined to a single species of host (Howard & Anson 1922). Copepods (Salmincola) that flourish on the gills of brook trout will not live on the gills of brown trout (Fasten 1913). In Scotland there is a warble fly that attacks deer but will not infest sheep (Mac Dougall 1934). Ichneumonids are quite restricted in their host relations (Mell & Henirich 1931). Many species of crustaceans (Caullery 1922), mites (Ewing 1912), mallophagans, myrmecophilous beetles (Wheeler 1907), and other animals are associated with a single host species, genus, or family. Chance (1922) says that an individual cuckoo usually has parasitic relations with one other species of bird. He describes one cuckoo that laid 21 eggs during a season, all except one in nests of the meadow pipit. On the other hand, some parasites are not confined to a narrow range of hosts. The American cowbird, *Molothrus ater ater*, lays its eggs in the nests of at least 141 species of birds (Friedmann 1934). The parasitic larvae of water mites occur on a variety of aquatic insects (Munchberg 1935). Jammes and Mandoul (1905) believe that the specificity that certain cestodes show for particular hosts depends on fluids within the host. They point out certain instances where bactericides are the same in different species of parasites that occur in the same species of host and different in a single species of parasite

that occurs in various hosts. Bactericides constitute one means of defense that hosts may have against invasion by parasites. A careful study of host selection has been made on a species of Microplecton, an insect that is parasitic on cocoon-inclosed larvae of another insect, Diprion, by Ullyett (1936). In this case the shape of the cocoon appears to be the factor that stimulates the parasite to lay its eggs on this particular host, though odor also plays a part. In all cases where parasites are adjusted to hosts there must be toleration of some sort. The fact that parasites are often associated with closely related species suggests that food and body substances may play a role in toleration. The frequent association of parasites with organs that are least vital is another factor. Adjustments between parasites and their hosts are, like all other adaptations, the outcome of long interactions among hereditary tendencies, variations, environment, and selection.

Reproduction of Parasites.—Parasites usually show a high degree of specialization in reproduction. There are more or less remarkable structural, physiological, and behavioristic adaptations for multiplication, fertilization, provision for offspring, entrance into new hosts, etc. (Fulton 1933, Zandt 1935). As among many free-living animals (rotifers, aphids), there is among parasites a pronounced tendency when conditions of life are favorable and food is abundant to multiply by asexual methods or parthenogenesis. The egg of a chalcid within the body of a host may produce many adults through polyembryony or germinogony (Patterson 1921, Brues 1921). Cestode tapeworms show an alternation of generations, the asexual proglottids in the intestine of the primary host budding off proglottids which in turn give rise to zygotes. Some cestodes have introduced another generation by the multiplication of the cysticercus in the secondary host (*Echinococcus granulosus*). Digenetic trematodes commonly have an alternation between parthenogenetic and amphigenetic generations, and there is among the former a considerable tendency among different, or even in the same, species to continue the production of individuals without the formation of zygotes. There are a number of cases of extreme sexual dimorphism among parasites. Woodruffe-Peacock (1900) discusses the reproductive peculiarities of the cuckoo in relation to parasitism. The female usually lays an egg on the ground,

takes it in her beak, and places it in the nest of her host, or she may lay directly in a nest if it is favorably situated. The egg is small and thus well suited to the nests of small birds. The female cuckoo may remove the eggs of the host. She or her young may shove the young of the host from their nest. The female does not leave her young to shift entirely for themselves. One braconid parasite is able to fly as soon as it leaves its cocoon (Kelly 1908). A female of this insect may mate within a minute and lay eggs within 4 minutes after she emerges. Weather has considerable influence on the life histories and periodic reproductive activities of certain parasites and hosts (Shelford 1926). In many ways the reproductive activities of parasites are adapted to particular hosts and particular conditions of life, which is, of course, more or less true of all adaptations.

Life Cycles of Parasites.—The life cycles of parasites are also often adapted in a high degree to peculiarities of hosts. In some cases the timing and relations of particular stages in life cycles may have been established long in the past, before one animal became a parasite on another. Two species of robberflies have a 3-year life cycle which corresponds to that of the June beetle. The larvae of these flies can exist for long periods without food and wander through the ground in search of the white grubs of the beetle (Davis 1919). The adult June beetles are largely nocturnal, and most of their parasites are the same. Many parasitic insects that infest other insects have shorter life cycles than their hosts (Withington 1909). According to Brues (1908), hymenopterous parasites often have easier methods of acquiring food, develop more rapidly than their hosts, and may enter another host if the first becomes unsuitable. Clausen (1923) has described a parasitic insect that lays eggs in tree buds, where they remain for about 11 months, only those in dead buds surviving. The larva attaches itself to a wandering ant (Camponotus) worker which carries it back to the nest. The parasitic larva then sucks blood from the larvae and pupae of its hosts. One hyperparasite bores through a caterpillar to find its host but does not emerge until its host leaves the body of its caterpillar (Brues 1921). The parasite Psithyrus winters over like its bumblebee host but does not emerge in the spring until the host has a well-established colony; the host queen is never killed until after she has begun to lay eggs, thus insuring a certain

number of workers to carry on the labor in the colony (Sladen 1921). Bees that harbor Stylops parasites emerge as adults earlier than others, and their parasites are thus ready to infest new hosts (Ulrich 1933). There are two strains of the Mediterranean flour moth, *Ephestia kuhniella.* One passes through a complete life cycle in 35–37 days at 32°C.; the other requires 62–65 days. The fast strain is less subject to attack by a braconid parasite (*Microbracon hebetor*) because it supplies nourishment for a shorter time (Payne 1934).

Hyperparasites.—There are many parasites that infest other parasites. These are most common among groups of insects such as braconids and chalcids. Near Chicago, Marsh (1937) collected and examined, 2,741 cocoons of Cecropia moths. Of these, 22.8 per cent had been destroyed by an ichneumonid parasite, 6.8 per cent by woodpeckers, 3.8 per cent by mice, and 3.1 per cent by a tachinid fly. He also found "5-linked chain of hymenopterous hyperparasites," which in order of rank were *Samia cecropia, Spilocryptus extrematis, Aenoplex smithii, Dibrachys boucheanus,* and *Pleurotropis tarsalis.* Four other hyperparasites were also associated with this food chain. In the nest of a black-capped chickadee (*Penthestes atricapillus*), two cowbirds (*Molothrus ater*) were present. Both of the latter were infested with hippoboscid flies (*Ornithomyia anchineuria*), and attached to the abdomen of one of these were two mallophagans, which perhaps thus obtained transportation from one bird to another (Herman 1937).

Methods by Which Parasites Establish Relations with Hosts.—Parasites have many methods of establishing relations with new individuals of their usual host species. The first step is to leave the host individual, and this is usually brought about through the production of propagative phases. The liberation of parasites may be accomplished by the death of the host (Myxosporidia), discharge from ulcers (Guinea worm), transmission to an intermediate host, passing into the eggs of the host, being taken into a bloodsucking animal, the discharge of eggs or embryos through the natural openings (anus, nostril, urethra, etc.), the eating of encysted stages in body tissues, the active migration of adult parasites, etc. After parasites have left one individual they must be able to enter another. Ransom (1906), speaking particularly of domestic animals, has given

an extensive account of methods of infestation. When a mammal dies, its lice creep out to the tips of the hairs and await the passing of another host. Dourine is transmitted from one horse to another during coition. Psithyrus finds its bumblebee host by odor (Sladen 1912). Some wasps allow themselves to be caught by tiger-beetle larvae. Then one of these wasps stings its captor to death, pokes it into its burrow, attaches an egg to it, and fills in the burrow. Withington (1909) describes an insect parasite that lays eggs on aphids. Its host runs away, but, after waiting a moment, it persistently keeps up the pursuit and finally deposits its eggs. Parasitic ants (Grosswald 1933) may gain entrance into the homes of ants by forcing their way and killing the queen; mites enter by clinging to workers (Park 1932). Flies that prey on halictid bees which guard the entrances of their burrows lay eggs on pollen masses that are being carried in (Rayment 1931). Parasitic water mites run about on the surface film until hosts come near them or attach themselves to resting pupae and renew their hold when an imago emerges (Munchberg 1935). Malarial parasites are injected into man's blood in the saliva of a mosquito. Filarial worms are also carried by mosquitoes but bore through the skin by their own efforts. Hookworm larvae enter man from polluted soil by boring through the skin. Most trematodes enter their primary hosts with food as encysted forms, but the cercariae of the schistosomes bore through the skin. The cysts of lung flukes (Paragonimus) commonly occur in crabs and crayfishes; those of the common liver fluke (Fasciola) are found on vegetation. Trichina and tapeworms enter man encysted in flesh. Acanthocephalans are ingested in June beetles by hogs.

Number of Parasites Occurring in Single Hosts.—The number of parasites that may infest an animal is sometimes remarkable. Practically every dogfish (Amia) supports 20 or 30 tapeworms. Sometimes portions of a fish's intestine may be actually lined with a velvety coating of small acanthocephalans. Howard and Anson (1922) found that fishes were capable of carrying from 250–2,500 glochidia without serious injury but usually had very much less. The number of chalcid larvae produced by polyembryony varies in certain species according to the size of the host (Brues 1908). Leiby (1922) found that one of these chalcids (*Copidosoma gelechioe*) averaged 163 to a host, which

was finally nothing but a shell containing pupae in separate compartments. Thomson (1911) tells of collecting 553 Pieris caterpillars, 422 of which died from the ichneumon parasites. In bank swallows' nests in New York, Stoner (1936) found young birds heavily infested with parasites. As many as 77 blood-sucking fly larvae, *Protocalliphora splendida*, occurred on one bird, besides mites (Atricholaelaps), fleas (Ceratophyllus), and biting lice (Myrsidea). Animals with permanent homes are more often heavily infested with parasites than those which travel about continually. Every drop of blood in a man's body may contain from 200–300 larvae of filarial worms; his intestine may support as many as 4,000 hookworms. The number of protozoans present in parasitized animals may of course be very large. Usually multiplying parasites do not increase to such an extent that they kill their host, but they may do so (Osorio-Rebellon 1931).

Effects of Parasites on Hosts.—Parasites produce various effects on their hosts. By taking food, secreting toxins, occluding passages, and in other ways they may retard growth, cause the host to live on in poor condition, become sexually impotent, assume new forms, produce galls, or die. Hosts often react to the presence of parasites by building up various defenses to combat them. The skins and the peristaltic movements in the intestines of vertebrates to a certain degree keep out or tend to pass out parasites. If the tissues of the host are infested, a fibrous investment may be formed by the host around the parasite. Leucocytes and antibodies also serve as deterrents or preventives for parasites. A host that has enough devices to prevent a parasite from establishing or maintaining relations with it has immunity. This may be natural or acquired. The black bass becomes immune to glochidia after passing through two to five periods of infestation (Arey 1923). Infested animals usually pass through a prepatent period during which no ill effects are apparent, then a patent period when parasites may produce more or less pronounced symptoms of disease. After this an infested animal may die, develop immunity and recover, or continue in a weakened state with a limited or large number of parasites. For a particular species of parasite one individual host may develop complete immunity, but another may be unable to do so. Some individuals show symptoms of disease

when others that harbor an equal number of parasites show none. There is much variation in the effects of parasites on hosts (Andrews 1934, Arey 1932, Becker 1934, Chandler 1934, Sheldon 1937). Highly organized animals may take various active measures to rid themselves of parasites or prevent infestation. The beaver has a specially modified louse claw, with which it combs its fur. The kangaroo rat avoids warble flies by strict adherence to nocturnal habits (Vorhies & Taylor 1922), and the reindeer escapes the same parasites to some degree by frequenting windswept coastal barrens during the summer. The pelicans along the coast of Peru rinse the insides of their pouches with sea water to get rid of bird lice. Many birds dust their feathers at intervals to irritate the tracheal tubes of arthropodan pests.

Many of the influences exerted by parasites on hosts are rather subtle and not clearly understood. Potts (1909) claims that the parasitism of male spider crabs by Sacculina causes the assumption of female characters. Most such cases of parasitic castration merely cause the continuation of juvenile conditions, or, in other words, a failure to mature. Crickets, termites, and ants are often sterile and unusually large when parasitized. Parasites in many cases undoubtedly cause alterations in the body fluids of hosts, introducing toxins which interfere with normal activities or substances that have other effects. They may extract substances that would normally be present.

Animal Galls.—Animal galls are produced on a variety of hosts by parasites. Corals are thus modified by crustaceans, worms, and other animals. Pycnogonids cause galls on campanularian hydroids, glochidia on fishes, copepods on ophiurioids and in sea urchins, myzostomes and other animals on crinoids, barnacles on sponges, etc. As in the case of plant galls, such abnormal growths appear to be caused by irritation due to the presence of living organisms.

Slave Makers.—Certain ants capture and enslave ants of other species and keep other animals in their nests for various purposes. A *Formica rufa* queen invades a *F. fusca* nest, kills any workers that attack her, and rears the young ants to work for her (Eidmann 1926). *Formica rufa* usually does not establish new colonies unless its slaves (*F. fusca*) are already present in an area (Gosswald 1933). The amazon ants (Polyergus), both queens and soldiers, make raids on *F. fusca* nests and bring

home broods which they rear to become slaves. These ants are quite dependent on their slaves, being unable even to feed themselves. They are obligate slave makers. In the European genus, Strongylognathus, slaves accompany their masters on slave-making raids on other species of ants. Ants of the genus Harpagoxenus are degenerate slave makers which show feeble ability to raid and capture slaves but have rather become social parasites. Other ants have degenerated into complete social parasites (Wheeler 1928).

CHAPTER XIV

ECONOMIC ECOLOGY

Economic Ecology.—There has long been interaction between man and other organisms on the earth. Some of these organisms have been beneficial, and others have been injurious to man. Since man has been able to carry along the ever increasing heritage of civilization from one generation to another, he has taken a more dominant position. He has transformed considerable areas of the earth's surface in order to make them more suitable to his needs. A savage gained his living in an environment without essentially changing it; but with the growth of civilization and the increasing influence of commerce and money, things that interfere with the activities of man have come to be pests, and many of those that lend themselves to man's support or pleasure have been fostered and increased. Today it is the duty of man as the present dominant species to consider carefully the plant and animal populations of the earth in order that they may long continue to furnish food and other necessities for the human race. Ecology is intimately concerned with the solution of this conservation problem, which is perennial. It will never be solved completely because conditions on the earth change continually and because the interests of all individuals are not the same.

Man has two activities that are more or less antagonistic. If he increases his numbers and his dominance, there is a tendency to eliminate organisms and habitats that may be economically productive. If he conserves his natural resources, he must do so by controlling his natural instincts for destruction or by inventing new means for increasing production. Savages are few in numbers and gain their living from essentially primeval habitats. A pioneer hunts, clears away timber, breaks the sod, and raises crops or flocks. After him come railroads and cities. Man destroys and plants, changes the soil, introduces new plants and animals, changes the vegetation cover by grazing his domestic animals, and in other ways transforms his environment.

Influence of Man on Environment in Scotland.—Ritchie (1920) has considered very thoroughly man's influence in Scotland. He discusses changes that came about through the introduction of sheep, cattle, and horses; those that came through deliberate destruction of animals for safety, food, skins, oil, the eradication of pests, and sport; those that came with the destruction of forests and the cultivation of soil; and those that were associated with the presence of new animals that resulted from commerce. Ritchie points out that, though large animals have gradually decreased, the total number of animals per acre has generally increased. He cites instances where rabbits, sheep, and goats have kept forests from developing. He also describes an interesting case where the protection of gulls on a moor led to the growth of grass and dock and a great decrease in the number of grouse. When the gulls were no longer protected, heather returned to the area, and grouse again became common. Forbes and Gross (1922) have pointed out that in Illinois birds are not changed to any extent by man's modification of their environment but seek out the habitats that most nearly resemble those they occupied before. Prairie birds come to live in pastures; thicket birds turn to orchards.

Resources of the Ocean.—The sea is a great reservoir where all elements necessary for life are to be found. Sea foods supply nutritive substances that are rare or absent in many land habitats (Taylor 1932). Practically all the products that man obtains from the sea are natural growths which cannot be increased by culture or fertilization. Food is obtained from fishes, molluscs, turtles, birds, mammals, crustaceans, various other invertebrates, and algae. Of all the food resources of man those least likely to be depleted and exhausted are in the pelagic region of the sea (Ritter 1918). Fertilizers are derived from seaweeds, whales, fishes, and other sources. Products from various marine industries furnish foods for poultry and other domestic animals. Clothing, furs, leather, buttons, pearls, and derivatives of algae that serve for stiffening come from the sea. Oils are furnished by fishes and whales. Ornaments and curios come from various animals. Algae supply agar, potassium iodide, and other substances. The oceanic fisheries of the world have been rather well studied and are more or less under international control (Russel 1932, 1934). The world consumption of sea foods is estimated at about 30,000,000,000 lb. annually (Taylor 1932).

Resources in Freshwater.—Freshwater habitats are much more limited than those in the sea. They in general produce more foods in shallow than in deep water, but large lakes and rivers generally support more valuable fisheries than small ponds and streams, though some of the fishes that most delight sportsmen are found in the latter. Swamps are valuable resorts for frogs, waterfowl, muskrats, and other animals. Some products produced in freshwater are of higher quality than those in the sea. For example, the clams from which buttons and pearls are obtained come largely from rivers in the United States and China (Coker 1919, Miller & McClure 1931), whereas the shells of marine clams do not make sturdy buttons, and few of them produce pearls of high quality. Freshwater habitats because they often have close associations with the habitations and daily life of men have intimate relations with his food, cleanliness, and health (Thienemann 1935).

Resources on Land.—Land plants are sturdier, more permanent, and generally of greater nutritive value than those in aquatic habitats. They produce strong timbers and concentrated nutrients in the form of seeds, nuts, starch-bearing bulbs and leaves, etc. Land areas are under much better control from the point of view of production than aquatic habitats. However, it must be remembered that in most parts of the earth only a small percentage of land is suitable for crops or pasturage. Often water and fertilizers must be supplied to make soils productive. Seasons are often more variable than in aquatic habitats, and crops may fail in some years and produce bountiful harvests in others.

Science and Industry.—Man's success depends on his ability to become adjusted to his environment, and every variation that helps or hinders his success is of economic importance. Yet scientific knowledge and research cannot and should not be entirely devoted to or dominated by economic considerations. Howell (1921) and Sumner (1923) have stressed the value of pure as well as applied science. Sumner (1910) says:

> To the reader who would demand an exact economic equivalent for the labor and money here expended our answer must be a more general one. Science and industry move together. Industry is helpless without the aid of science, and the greatest industrial progress is at present being made by those countries which realize this fact most fully. But science

can never prosper if forced to play the rôle of a servant. She must be free to pursue her own ends without being halted at every step by the challenge: *cui bono?* The attempt to restrict our scientific experts to problems of obvious economic importance would be equivalent to depriving ourselves of their services altogether. It is today accepted as a commonplace that all the great discoveries of practical value have resulted ultimately upon principles first brought to light by the student of nature.

Science is related to industry and economic problems, at times as a commensal, at times as a symbiont, and, it is regretfully admitted, sometimes as a parasite. Ecology, like other branches of science, should not be dominated by industry, but, on the other hand, it should not ignore industry. Environment is and will continue to be modified by man and his civilization. The world will never be primeval again, and ecology must "carry on" in the world as it is and will be. It, therefore, seems appropriate to devote this chapter to a brief consideration of the economic relations of ecology. Ecology should be "useful" in connection with such practical matters as soil conservation, land classification and utilization, resettlement projects, all farm sciences, fisheries management, practically all phases of conservation of natural resources, reforestation, range rehabilitation, wild-life management, medicine and epidemiology, anthropology, and social sciences (Taylor 1936*a*).

Food Production.—Man requires a continual supply of organic food, the constituents of which have a reasonable degree of balance in chemical constitution and calorific value, and which contains an adequate supply of vitamins. Plants, directly or indirectly, are the basis for the chief foods consumed by man. Waterman (1917) has pointed out that ecology can contribute to plant production by developing general principles that may improve quality or increase productivity and by furnishing knowledge for specific crop problems. Ecologists should know the optimum conditions under which particular plants live and how such conditions may be preserved or brought about. The knowledge of the principles of production is much better for those crops that grow on land than it is for those that develop in water. Even scientific men are barely beginning to speak of aquiculture in terms of bushels or pounds per acre. With greater knowledge it will doubtless be possible to exercise more or less control over

production in bodies of freshwater that are limited in extent and in favorable areas in the shallow waters of the ocean, but the great reaches of the open sea will probably long remain free from regulations of civilization, except those that relate to restrictions of fishing. Foods have exercised profound influence on the types of culture that man has developed in various regions (Bews 1935). There have been primitive food gatherers, plant cultivators, herdsmen, fishermen, etc. Favorable land areas on the whole produce more per unit of area, either flesh or vegetation (James 1929), than water. However, there is rather uniform production throughout comparable areas of water, whereas many tracts of land are nonproductive. A land area may produce 100–300 lb. of flesh annually, and a favorable body of freshwater may approach this. Such products as wheat or corn may yield 800–1,700 lb. per acre.

Increasing Food Resources.—The increase of food resources may be accomplished by the discovery of new foods, better methods of propagation, better ability to forecast favorable seasons or years for the gathering or producing of particular foods, the education of persons concerned in production, the limitation of the use of animals during comparatively valueless stages which may be of greater value at other times. Oceanographic exploration led to the discovery of the fishing grounds for the delectable tilefish and the valuable deep-water prawn fisheries of Norway. The scientific study of the life histories and migrations of the salmon along the Pacific coast of America has made it possible to predict years when there will be heavy or light catches. The European oceanographers have been able to make similar predictions for mackerel fishermen through scientific knowledge concerning the relation of sunlight to the production of diatoms and copepods. In many countries there are laws that limit, at certain periods, the use of animals for food, when such use may be expensive because animals will be of greater value if allowed to grow to larger size or because the use of certain individuals may interfere with the normal increase of the species concerned. In aquatic habitats especially, there is need of greater knowledge of the fundamental principles of production. This largely because many aquatic plants and animals are microscopic and reproduce rapidly. On land the approximate rate of increase of food plants and animals is rather well

known, but the rate of growth and of multiplication of most aquatic organisms and the factors that control such increases are not understood. Production on land is easier to understand also because it is confined to a rather thin stratum at the surface, but aquatic habitats may be more or less productive at all depths. Increase in productiveness depends on the knowledge of the effects of fluctuations in various ecological factors. Food must be produced in an environment.

Production may be decreased through the introduction by man of influences that make the environment unfavorable for particular food animals, by depletion through the removal or destruction of too large a number of animals in a particular area, and by other acts of man. Pollution and dams have decreased the number of fishes taken from many streams, and no other food resources compensate for such losses. The buffalo once grazed in countless herds over the prairies of North America but can never do so again, and their place has been taken by beef cattle. These two instances illustrate the contrast between the results of the exploitation of natural food resources in terrestrial and aquatic habitats. Agriculture is developed to such a degree that it easily supplies food that is equal to or exceeds that which an area furnished under primeval conditions, but aquiculture is rarely able to do this. From another point of view, water areas for the production of human food have the advantage in their present state of development that they require little labor except that of gathering the crop. One service that ecology can perform is to point the way to more scientific methods of aquiculture. At present the human race takes natural products from aquatic habitats without much knowledge or thought of conserving and increasing production. In the oceans, the cooler parts are most productive of human foods and most difficult for navigation. All aquatic food resources are being slowly but surely depleted by overfishing. Such depletion is, of course, slower in the ocean than in freshwater.

It is possible that civilization may in time reach such a state that man will cover the whole earth with his activities; that available energy may be utilized to such a degree that food production will be entirely under control through the use of artificial light, the exploitation of domesticated plants and animals, etc. But if such a state is ever reached, it will be far in

the future, and many generations must worry over the relations between food production and environment.

Increasing General Productiveness.—Agriculture is in general well organized, and production approaches maximum possibilities through the use of cultivation, fertilizers, and irrigation. In aquatic areas productiveness is not always so successful. In the ocean a few crops, such as algae, sponges, and mussels and oysters, are harvested from definite cultural areas, but most marine products are the result of natural growths. In freshwater there have been various more or less successful attempts to increase production by operating "farms" for frogs, alligators (Kellogg 1929), muskrats, other animals, and plants. Production has been increased by rearing and supplying natural foods for aquatic animals, *i.e.*, chironomid larvae (Sadler 1935), cladocerans (Needham & Brown 1933), May-fly nymphs (Neave 1932), wild duck foods (McAtee 1917), etc. By improving waters or making use of appropriate areas it has been possible to increase production by the use of fertilizers (Langlois 1933) or aquicultural methods for such types as clams (Coker 1919, Howard 1922), fishes (Johnson & Stapleton 1915), and other animals. By education and advertising, new foods and products have gained recognition and markets. Whale and reindeer meat (Palmer 1934) are now offered for sale in the United States, canned or frozen. The mud puppy has been suggested as a more delectable food than frog's legs (Pearse 1921). Such industries as that dependent on the guano birds in Peru have been organized and to some degree made safe for future generations (Coker 1910).

Environment and Culture.—Huntington (1922) has made it clear that man is influenced to a considerable extent by his environment. Not only is this true of the general condition of man in regard to health, but the amount of work that man may accomplish from day to day and his attainments through successive generations are controlled more or less by climatic conditions. In other words, the type of civilization that man develops and the level that any type may attain depend on environment. Areas that have variable climates and favorable conditions of humidity have often permitted the development of a high state of culture; in arid areas with monotonous climates the human race is usually in a low state of civilization. Climate exerts influences on man through effects produced on his physiological condition, so that he

may be in one locality lazy, unambitious, worried, and unproductive and in another locality quite the opposite. Such effects are also often brought about because the environment is favorable for the propagation and spread of diseases. The relations of tundra, temperate forests, fertile prairies, grasslands, hot deserts, monsoon regions, tropical forests, summer rains, and altitude to settlement, food-supply industry, manufactures, transport, and growth of populations is discussed by Sheamur (1931).

Environment and Disease.—Many animals in an environment may spread human diseases or those of animals, and these are often unsuspected agents. Certain salamanders that live in springs may spread typhoid (Kline & Fuller 1932). In Ceylon various species of fleas are associated with certain specific climatic conditions, and the one that carries plague is definitely restricted to moist forested areas where conditions for development of larvae are favorable (Lefrou 1931). Tsetse flies are strictly diurnal in their activities and hence do not attack men who are asleep at night (Nash 1933). The snails that carry schistosomes may hibernate through long dry periods and maintain their infestations (Barlow 1933). In regions where lime is lacking snails and digenetic trematodes are absent (Layman 1933). The abundance of many insect pests that attack crops is greatly influenced by weather and hence varies in different years (Farquet 1931, Fredericks 1933, Ingram & Bynam 1932, Payne 1933, Shelford 1932, Smith & Kelley 1935, Whitcomb 1933, Sweetman 1933). The ecology of human diseases has recently taken an important place in the study of medicine (Reed 1935, Strong 1935). Man's adjustments and maladjustments to various climates and diseases associated with various types of environments have attracted attention in this connection.

Water Supply and Pollution.—The bodies of freshwater from which man derives the water to supply his physiological and industrial needs and into which he discharges various wastes which result from his activities also serve as habitats for many aquatic organisms. Knowledge of the interrelations between man and the organisms in freshwater is, therefore, of prime importance. Often there is conflict between the interests of particular industries or other activities of man and those of freshwater animals. The conditions that maintain pure, healthful streams, ponds, ocean, and lake shores often conflict with those that are favorable

to the cheap disposal of sewage and factory wastes and to the development of water power.

A sanitary engineer looks upon sewage disposal as a legitimate function of a river. The discharge of a large amount of organic material into a stream may act as a fertilizing agent and result in a great increase in the quantity of animal life; it may have little effect because the stream quickly exercises its powers of self-purification; or it may produce pollution. The discharge of sewage into a stream should be undertaken with forethought and knowledge of the probable effects. Forbes (1919) has made a rather extensive study of the effects of the sewage from Chicago on the Illinois River. Purdy (1923) has made similar investigations in the Ohio River; and Suter and Moore (1922), in the streams of New York. Forbes found that most species of fishes were driven downstream and that the upper reaches of the river became in a sense an aquatic desert. The fishing for a time improved below the region of pollution and later decreased. Baker (1920) noted that sewage in the Genesee River caused a complete absence of snails, but the river was slowly repopulated when the amount of sewage was reduced. On the Danish coast the bottom about sewer outlets is devoid of life for some distance. (Blegvad 1932). Sewage in streams, if it has been thoroughly treated to remove toxic substances before entering, may be beneficial to fishes by contributing nutrients (Hubbs 1933). Fibrous wastes, such as wood pulp, do not appear to be particularly injurious to fishes if unaccompanied by toxins (Cole 1935). Jackson (1922) studied the marine fishes along the coast of New Hampshire and concluded that certain species had been exterminated. The unfavorable conditions in this instance were largely brought about by the construction of dams across rivers; and the pollution of the littoral water, by wastes from a navy yard and oil-burning steamers. Birds resist cold by means of air spaces inclosed in their plumage. When their feathers are saturated with waste oil discharged from ships, they lose heat to the surrounding water and succumb to cold (Portier 1934).

Shelford (1919, 1920) has stressed the importance of the study of pollution. He suggests that many substances that now do harm as wastes and are therefore expensive to the community as a whole may, if saved, be made to pay wholly or in part for the expense involved in developing and using new methods of dis-

posal. Suter and Moore (1922) have classified trade wastes in the following order according to their degree of toxicity to fishes:

Sawdust and treated sewage—no dilution required.
Raw sewage and fiber factory wastes—require dilution of 1:10.
Spent dyes and paper-mill wastes from 1:10 to 1:100.
Gas manufacture wastes and wastes from bleacheries—from 1:100 to 1:1000.
Caustic lime and mercuric chloride—1:1000 to 1:10,000.
Lime, strong acids, gas tar—1:10,000 to 1:100,000.
Copper sulphate, bleaching powder—greater than 1:1,000,000.

Pests.—The problems relating to the control or eradication of pests are, as a rule, ecological. The efforts of man to combat animals that cause economic losses are often of no avail because the ecology of the problem is not thoroughly understood. A struggle against an animal pest is now commonly initiated by a detailed study of behavior, habits, and life histories. The worst pests among plant lice are said to be among species that migrate readily. Satterthwait (1921) observed that billbugs injured corn in a certain field each year but that after an adjacent area of cattails, which harbored the pest, was plowed under, there was no more trouble. Cooper (1922) found that birds and certain plants had important relations to the control of white-pine blister rust. He observed that forest birds did not feed on fruits and scatter seeds to any extent but that those that frequented open ground commonly did so. The wild gooseberry was thus planted in pastures and other cleared lands and there harbored the blister rust. Wheeler (1911) tells how ants help to increase aphids on melon vines by destroying the enemies of these pests. Barber (1925) makes the following comments on the corn borer:

> Among the factors which may be held accountable for the decrease of numbers of the European corn borer in New England in 1923, the subnormal temperatures which prevailed during the oviposition season in the late summer played an important part. The probable longer periods of life of adults, caused by low temperatures, served to spread oviposition over a relatively longer period, which was favorable to the development of the egg parasite, *Trichogramma minutum* Riley, and the relatively fewer eggs deposited per female probably served to increase the importance of the parasite.

This is ecology. Pests are scattered all through the animal kingdom; protozoans often cause epidemics among fishes; hydras

devour eggs in hatcheries; crayfishes penetrate dykes and devour crops; shipworms and boring crustaceans do great damage to piling, ships, and other wooden structures in the ocean, and termites carry on similar activities on land; many insects attack crops and other structures; wild rodents steal grasses from man's domestic animals; etc. When species are introduced into new localities where they are free from their usual enemies and parasites they often become pests, *e.g.*, gipsy moth, boll weevil, Mediterranean fruit fly, muskrat in Bohemia, mongoose in Haiti, rabbit in Australia, English sparrow in America, etc.

Methods of Combating Pests.—Pests are commonly attacked by man during those periods in their life histories when they are more vulnerable or more easily accessible. Rats are hunted with ferrets; foxes are pursued with dogs. Against insects, parasites and predaceous enemies are commonly employed. Such allies of man as ichneumons, evanids, chalcids, tachinids, and fungi are reared and scattered about in localities where they will be of most value. The detailed knowledge of the habitats of various species of mosquitoes in regard to habitat selection and environmental conditions has been of great value in campaigns against malaria, yellow fever, and filariasis. Connor (1921) was able to free Guayaquil from yellow fever by using minnows which cost about half a cent each. In buildings, appropriate fumigants are used to destroy pests (Black & Cotton 1937), or repellant substances are employed which cause animals to leave the premises. Imms (1937) gives an excellent account of recent advances in methods of control of insect pests.

Damage by Pests.—The amount of damage done by pests is often astounding. Sometimes such damage is quite apparent, but in other cases it may remain unnoticed. The fact that shipworms and other pile borers caused losses of $15,000,000 along the San Francisco water front during the years 1920 and 1921 attracts attention. On the other hand, grasshoppers sit in every field and, unless present in great numbers, remain unnoticed. Shull (Ruthven 1911) found that in eastern Michigan, grasshoppers in a field of bluegrass and timothy averaged 12.9 in. apart and that a single grasshopper ate 50.4 in. (127 mg.) of grass-blades in 24-hours. He says: "I compute that the grasshoppers in a field of 27 acres may, in a grasshopper year, devour 1 ton of cured hay per week." In Oregon pea fields the following

numbers of species of insects were found: (*a*) beneficial: 4 Hemiptera, 24 Coleoptera, 1 Neuroptera, 2 Hymenoptera; (*b*) injurious: 4 Orthoptera, 2 Homoptera, 21 Hemiptera, 6 Coleoptera, 2 Lepidoptera, 3 Hymenoptera; and (*c*) doubtful: 2 Hymenoptera, 2 Coleoptera, 5 Hemiptera. The number of pea weevils ranged from 6,534–1,580,356 per acre; average 307,094 (Larson & Hinman 1932).

Pests Due to Man's Activities.—Some animals may become pests because they are protected by man. Fishing is often restricted by law to sportmen's methods; undesirable fishes are thus not caught and increase beyond their normal numbers. Geese and ducks are protected in Alaska, where they do much damage by destroying herring eggs. Such conditions raise problems that should be the subject of ecological study (Anderson 1934, Marshall 1934, Storer 1934).

The introduction of animals into new areas is often associated with disastrous consequences to man. Familiar examples are the introduction of the rabbit into Australia, the mongoose into Haiti, and the English sparrow into the United States. The offspring of four American muskrats introduced on an estate near Prague multiplied and finally became such pests that stringent laws were passed to limit their spread (Ulbrich 1930). Huey (1925) has given a graphic account of the results of the introduction of goats on Guadalupe Island by whalers. In 1923 the condition of the island was well described as that of a "biological sepulcher."

> The place proved to be a goats' paradise, for with plenty of low herbage and not a single enemy, they had life their own sweet way. They increased by tens of hundreds, devouring everything green that was in sight and gnawing their way into the very heart of the primeval forest. . . . In spite of the damage to Guadalupe Island's bird and plant life that must already have been wrought by mice, cats and goats, Dr. Edward Palmer, well-known government botanist, who visited it in 1875, described it as a "naturalist's paradise." It would seem, however, that he arrived only in the nick of time to secure a few of the vanishing birds and plants and thus preserve their memory forever in the annals of science.

Animal Products.—Animal products that depend on the exploitation, and often also on the slaughter, of wild animals

have usually decreased steadily until the supply has become so depleted that legal restrictions have been necessary. This has been the history of sealskins and other furs, shells and pearls, fishes, whales, plumes, and other natural resources. In some cases man has introduced factors into the environment that have made conditions unfavorable for the animals concerned, but most such resources have been depleted by overhunting and overfishing. Some animal products do not require the death of the animals furnishing them. According to Coker (1919) a million gannets are capable of producing about 11,400 tons of guano each year on the coast of Peru, and even more is deposited by cormorants. A large part of the revenue received by the Peruvian government is derived from the droppings of these birds, and they are carefully protected.

Domesticated Animals.—The environment of domesticated animals can often be adjusted so as to be more favorable. In general, animals do best when they are provided with room for exercise, shelter, and proper food. A ration must not only contain proteins, carbohydrates, fats, water, and minerals but also possess a naturalness that is supplied by green foods containing vitamins. Poultry also requires light. Fox farms that are kept free from hookworms are generally most productive. In a locality where ticks are prevalent, cattle may be deficient in milk flow, flesh, and reproductive capacity. The frequent dipping of animals or the eradication of ticks by other means may transform an unfavorable environment into a favorable one. In some countries where ticks are prevalent zebus have been crossed with common cattle, and a short-haired race that does not readily harbor ticks has thus been introduced. Other attempts to produce domestic animals that have greater resistance to unfavorable environmental conditions have been made by crossing yaks, buffalo, and other animals with domestic cattle. Crosses between horses and asses have produced large and sturdy draft animals. The growth of the dairy industry in New Zealand furnishes an excellent illustration of how the successful raising of domestic animals depends on environment. In many parts of the earth man has learned by experience what types of animals are best suited to local climatic conditions. Agriculture now has a considerable body of such knowledge, and more is being accumulated continually.

Soil and Soil Products.—Every farmer knows that certain soils are suited to certain crops, and considerable progress has been made in the scientific study of soils. A farmer can have soil samples analyzed and receive a prescription that will enable him to apply appropriate materials to make it more productive. The study of the animals that live in the soil and the effects of these on soil productiveness is still new. Soil bacteria are rather well known; soil protozoans and nematodes have been studied somewhat, but much remains to be learned concerning the ecology of soil organisms.

One of the great injuries that man has perpetrated is the denudation of the soil. It may take long ages to build up a humus soil that can support the climax plant formation for a locality. When man removes the vegetation, the nutrition is washed away and leached out. It may take centuries to repair such damage. The loss of vegetation may also decrease the water-holding capacity of the soil, make a dearth of food and shelter for animals, and be an important cause of disastrous floods. Recent observations indicate that the ashes resulting from forest fires may cause the death of trout in the streams that drain burned-over areas.

Conservation.—Conservation is concerned with the preservation of natural habitats, the keeping of the environment suitable for human and animal habitation, and the utilization and preservation of natural resources.

Preservation of Natural Habitats.—The preservation of natural habitats is important for scientists because primeval conditions are essential for certain types of ecological study. It is also often associated with the preservation of species of animals that depend upon a particular environmental complex and cannot adapt themselves to areas that have been occupied by the activities associated with civilization. In many cases forests have been wastefully cut away and swamps have been thoughtlessly drained when untouched, natural habitats would have been of more value to the human race. Natural areas have great value in relation to the pleasure, recreation, and health of men. Such tracts when wisely administered may pay dividends to many instead of furnishing a living for a few. Natural areas such as national parks and forests should be so administered that they may serve for recreation, scientific study,

and production (Adams 1931, Wright 1933). Such agencies as the U. S. Biological Survey (Gabrielson 1937) have a large organization and carry on studies relating to wild-life status and management; economic aspects of wild life; fur conservation and restoration; wild-life disease control; wild-life refuges; migratory water-fowl restoration; wild-life law administration; and control of rodents, predators, and other undesirable animals. When man changes environmental conditions a dynamic climax balance is disturbed, and appropriate adjustments must be made (Smith 1932).

Keeping Environment Fit.—As the earth becomes more thickly populated it becomes more necessary to keep natural habitats from being ruined by carelessness or the by-products of man's activities. A littoral clam may flourish when water is contaminated and laden with refuse, but a fish like a herring requires pure water and open spaces (Fraser 1929). Barren aquatic areas may be stocked with appropriate plants and animals and thus brought to productiveness long before they would otherwise mature (Pearse & Terrell 1920). When a great dam like that at Keokuk on the Mississippi River is constructed, conditions above it are profoundly changed, and thought must be taken as to how to rehabilitate the affected area. The flow of water becomes slower; silt is deposited over the bottom; certain animals are killed and must be replaced by others (Ellis 1931). The removal of soil cover on land areas permits denudation and if not corrected leads to impoverishment of soil, floods, and other evils (Silcox, Lowdermilk, & Cooke 1937). A farm may not only be a place to produce human foods but if wisely managed may also be a refuge for wild life (Grange & McAtee 1935).

Utilization of Natural Resources.—Every locality inhabited by man has certain natural assets which give it some wealth. The arid climate of Peru makes possible the conservation of the great deposits of guano from sea birds, which would not be possible if there were continual rains to leach out and wash away such remains (Coker 1920). Natural resources should be so used that man may now gain the greatest benefit from them but not so that they are destroyed without thought of future generations. This is especially true of the wild life, both plant and animal (Woodbury 1937). Some animals (such as the great auk, passenger pigeon, and heath hen) have been exterminated in recent times. Great progress is now being made in fostering

and increasing wild life. Leopold's (1933) book "Game Management" is a fine example of modern applied ecology. It deals with shelter, food, predators, economics, and ethics.

Preservation of Natural Resources.—The food supply and happiness of man depend to some degree on the conservation of natural sources of supply. The protection of watersheds in the western United States is necessary to preserve pasturage and prevent erosion and floods (Bailey 1936, Bennett 1935). The increase of aquatic resources by the use of ponds and reservoirs, and the conservation and regulation of those already available is essential for future food supplies (Coker 1915). Man by his activities has greatly decreased animal populations, and some of these may at least in part be rehabilitated if proper measures are taken (Storer 1932). Such animals as deer might find appropriate habitats in areas that are now nonproductive.

Obstacles to Conservation.—One of the worst obstacles to conservation is a lack of uniformity in the laws of contiguous states or countries. If a fisherman in one state is not allowed to catch fishes of a particular species that are less than 10 in. in length, although his neighbor in a state across the river can keep fishes of the same species that are 8 in. long, he naturally feels like breaking the law. If the sale of short lobsters is prohibited in one state and ignored in an adjacent state, the traffic tends to prevail in both states.

Another great obstacle to conservation is business "interests." Persons interested in making money from a particular natural resource may obtain concessions or have favorable laws passed that injure the community as a whole, and such privileges often pass unnoticed or without interest by those who are injured. In general, the size of fishes that may be sold has been continually made smaller in order to continue established business or to expand it. A lack of fish foods, paper pulp, and other products that might be conserved is threatened by lack of interest or thought.

It is possible that future generations may divert all the water from Niagara Falls in order to produce power. Perhaps such use of this natural resource may be for the general benefit of the human race. If such a change does come about, however, it is to be hoped that it will result from careful consideration by scientists, altruists, and businessmen, not as a result of privileges obtained by "special interests."

CHAPTER XV

TEACHING OF ECOLOGY

Definite Plan Essential.—A course in ecology, perhaps more than in any other field of biology, should be carefully planned and organized. If field trips do not have a definite purpose they may become picnic holidays which are of little value. The work for each week and each day should be carefully considered and carried on outdoors as much as possible. All men enjoy hunting and collecting. Such activities satisfy primitive urges which have been handed down from past ages. Those with a little learning also enjoy being able to name things that they find. Students in an ecology course should have a good time; but ecology is more than collecting and naming. It should be constantly kept in mind that ecology is concerned with the relations of organisms to environment. Systematic biology should be kept separate from ecology. It is not desirable for students to spend much time classifying the animals and plants encountered. A teacher should know and give them names and thus allow them to devote their time to ecological work. A course should include field observations, laboratory work, lectures, assigned readings, and reviews by students. In any advanced course it is desirable to have various students working on different things at the same time. For example, during a certain week one student may be responsible for keeping records of daily soil temperatures and humidity records in a forest, while another makes similar observations in a pasture, a third makes appropriate records for a lake, and a fourth records insects that visit a particular species of flower. In the following paragraphs suggestions are made that may be of value to those who are attempting to give courses in animal ecology. They of course are only a small part of things that may be attempted. Teachers with originality will think of "more and better" ways of presenting their offerings. Every teacher should plan his own course.

Alpine and Arctic Faunas.—Those who are fortunate enough to live near or in mountains may conduct excursions to elevated situations and study the communities; but when this is not possible, studies may be made from literature. Brooks, waterfalls, timber lines, glaciers, and differences between slopes that face in various directions are of special interest. Arctic faunas are beyond usual courses except in literature, and there is much of it available.

Alternation of Generations.—Along seashores various stages in the metagenetic cycles of coelenterates may be found. In freshwater it is possible in many localities to collect snails in which sporocysts and rediae of trematodes occur, and from which cercariae may be reared. Aphids, cladocerans, and rotifers may also furnish material for the study of heterogenesis.

Behavior.—The behavior of animals in nature or in laboratory, where conditions may be better controlled, may be studied with profit. When possible, animals that give rather clear-cut and definite responses should be selected for study. For example, mealworms, earthworms, and planarians usually give quite definite responses to light. In the field the death-feigning of certain bugs and "puff adders" is noteworthy. Endless observations may be made on the behavior of animals: the differences between male and female birds, the differences between soldier and worker ants, defense of territory by animals that occupy definite home areas, etc.

Climate.—Students may carry on routine observations on rainfall, humidity, temperatures, wind, and other matters. One way to start off a course is to have students plot climographs or hythergraphs (Shelford 1929, p. 18) which show ranges of climate for localities where they will carry on work. This gives them general ideas about their environment. Data may be obtained from the district summaries issued by the U. S. Weather Bureau.

Color.—Models may be used to illustrate Thayer's and Hingston's ideas on principles of coloration. A lively discussion will result if a day is set aside and students report on the works of Poulton (1890), Thayer (1909), Longley (1917*a*), Carpenter (1920), and Hingston (1935). A class may then be sent afield to observe and collect material for a second discussion. This may be supplemented by museum specimens that raise questions.

Competition.—Struggles among various species may be observed in protozoan cultures, and competition for space to live among such animals as oysters, barnacles, and fiddler crabs along beaches. One way to obtain material for discussion is to send students forth to secure any observations that they can for themselves.

Consortes.—The survey of various animals for commensals, symbionts, and parasites and the relations of such animals to their hosts are of interest. In any locality there may be fishes, frogs, insects, or other animals that will yield enough consortes to be acceptable for classwork.

Discussions.—No advanced course should progress without opportunity for discussion by all members of the class. The work of a course should be broken up into units, and the class given a chance, say every week or two, to raise questions and talk about what has been presented. It is desirable to have outlined and given to students a few general questions bearing on recent work. Perhaps all these cannot be discussed, but they at least give students some idea of what a teacher thinks is going on.

Dormancy.—Dormant animals may be found and observed in the field, or animals may be treated experimentally in field or laboratory.

Economic Ecology.—Such matters as pests and diseases may be studied by assigning various papers (*e.g.*, government bulletins) and in connection with them having various students study such situations as flour mills, crop plants, domestic animals, warehouses, granaries. Larger topics, such as erosion, game refuges, and conservation, often furnish interesting subjects for demonstrations and reports.

Factors.—There is endless opportunity for students to make observations in field and laboratory on the distribution of animals and ranges of toleration in relation to temperature, light, water soil, and other "factors," as described in Chapter IV.

Field Work.—Field trips in a course should as far as possible cover a typical series of marine, freshwater, and terrestrial habitats. Observations should be made on weather and other significant environmental conditions in each case. It is desirable for a teacher to have a card catalogue of species in each locality visited, so that students may at once have the names of plants and animals encountered. As has been stated, each trip should be carefully planned in advance and have a definite object.

Foods.—The foods of animals may be studied by making observations in the field or by examining the contents of enterons. The food brought to nestling birds may be readily observed with binoculars. For the study of foods already eaten it is desirable to use fresh, not preserved, materials; these are less distasteful to handle if kept wet and teased with needles on a glass plate under a binocular microscope. Food preferences may be studied by offering various types of foods and observing the amounts of those consumed.

Galls.—Galls may often be brought into a laboratory, and the makers reared to maturity if they are kept in good condition.

Geography.—Zoogeography has definite relations to ecology. The reading of general papers or those on particular regions may help in an understanding of a locality.

Homes.—The study of the populations of the homes of animals and relations of owners to and within them offer excellent materials for study. There is wide variety, from ant's nests to bear's dens.

Great Realms.—Oceans show a great variety of specific habitats and offer opportunities to study differences in populations with variations in salinity, together with many special problems. Freshwater furnishes many small habitats, such as springs, brooks, and ponds, that are limited in extent and therefore readily understood by students. Stratification and gases are often of interest in aquatic habitats. Land areas are readily accessible and can often be studied without such special equipment as required for water habitats.

Lectures.—The function of lectures in an ecology course is to contribute unity and introduce illustrative material not available in the locality where a course may be given; hence they may profitably be illustrated. They cannot take the place of observation, reading, and discussion but should supplement such activities.

Life Histories.—Life histories of insects and other animals furnish excellent illustrative material for the study of adaptation and adjustment to various types of environment. The ranges of toleration for the eggs, larvae, pupae, and adults of mosquitoes or June beetles, for example, are quite different.

Migrations.—Migrations offer good opportunity to support reading with specific field observations. If continued in one

locality for several years, records of the times of arrival of birds, the breeding of amphibians, and other seasonal progression phenomena become of great interest, especially if correlated with observations on weather.

Plant Consortes.—Animals associated with plants offer many opportunities to study relations. They are for pollination, food, shelter, seed dispersal, etc. A student may profitably study and report on all the animals associated with a single species of plant, all the insects that visit a single flower, or other similar relations.

Quantitative Studies.—The number of animals present in various habitats is of interest. Botanists have long used quadrats for estimating plants on land areas, and such counts may be made of animals. In water, counts may be made by using closing nets, taking volumetric samples with pumps on pipettes, and other methods. Counts of animals in soil are often desirable.

Records.—A student in an ecology course should keep a notebook. Such a book should have stiff covers and be small enough to be easily pocketed (say 5 by 7.5 in.). It should be covered with bright-colored oilcloth, so that it will not be greatly injured by rain and may be easily discovered if misplaced outdoors. A rubber band cut from an automobile-tire tube will keep it closed and retain a pencil within. In the field, notes should be taken on only one side of a page, thus leaving space for later interpolations of information concerning identifications and other matters, such as titrations for oxygen performed in a laboratory. It is usually desirable to make notes on weather and habitats. Each locality studied on successive days should be given a serial number. The numbers may be put in containers with specimens, and much label writing is thus avoided. Some observations are best recorded on special sheets. In making routine examinations for consortes a single form sheet should be used for each host. For observations on behavior of animals under experimental investigation individual graphs that show movements are useful (Shelford 1917*b*). Some types of behavior may be recorded on kymographs.

Reading Assignments.—In any advanced course it is desirable to acquaint students with classical literature bearing on the subjects under discussion. Readings may be assigned for dis-

cussion at intervals, along with materials from lectures, reviews, and field and laboratory observations.

Reports and Reviews.—Reports by students of observations and reviews of noteworthy publications are, if rightly managed, an important element in contributing interest to an ecology course, but if poorly presented may have the opposite effect. They should be carefully planned, digested, and outlined before being given.

Rhythms.—Tidal, daily, lunar, and annual rhythms are interesting subjects for study. The activities, behavior, and stages in life histories during such cycles may show correlations between internal and external cycles or other matters of importance. Periodism may or may not be associated with environmental cycles.

Sex.—Sex ratios, sex control, sexual dimorphism may be made the subject of class study. Rotifers, cladocerans, and aphids may have sex ratios changed by environment. Some parasites well illustrate dimorphism, and social insects may be used to illustrate castes.

Social Life.—Termites, ants, bees, wasps, and a few other insects may form the basis of observations on societies and the consortes that usually accompany them.

Societies.—The biota in any region or limited habitat and the interrelations within it are proper subjects for study.

Soil.—Astounding numbers of small animals live in soil. Surveys and studies of temperatures, moistures, profiles, etc., are of unusual interest.

Succession.—The changes that occur as pioneer communities gradually give place to climaxes may be suited in nature by comparing habitats in various stages of progression, in small artificial habitats introduced into particular environments or in small amounts of culture media. A cubical cement block may be placed in marine littoral habitats with four faces oriented toward the points of the compass, and the development of organisms on the surfaces studied. A protozoan culture made by inclosing boiled hay in a covered jar constitutes a little world in which successional changes may be observed and measured.

Surveys.—Various types of surveys constitute the chief basis for ecological knowledge. One way of terminating an ecology course is to assign each student a special problem on which he

is to make observations and prepare a report. This may be a broad or a limited habitat, *i.e.*, to survey a forest, a brook, a swamp, a single species of plant or animal. Surveys of habitats should include data on both physical factors and biota.

Territory.—Crustaceans, insects, birds, mammals, and some other animals defend definite territories. Such behavior may be investigated in the field.

Tropical Faunas.—Animals in the tropics are unusual in some respects. If they cannot be studied firsthand, students may become acquainted with them through reviews or assigned readings.

CHAPTER XVI

ECOLOGICAL METHODS

The writer planned a chapter that would include a rather full account of the principal methods used in ecology—and even started to write it—but it was apparent that such an account would either be a very limited, superficial mention of such methods or, if thoroughly and carefully done, would itself make a work far beyond the size of the present volume.

Sources of Information.—Such large works as Abderhalden's (1922–) "Handbuch der biologischen Arbeitsmethoden" give much information on methods. In the investigation of the sea, books like those of Harvey (1928) and Murray and Hjort (1912) will be found useful. For the study of freshwater habitats, Welch's "Limnology" contains a good review of methods, and Shelford's (1929) "Laboratory and Field Ecology" has many excellent suggestions. For land areas Shelford's book will again be found valuable, as will Weaver and Clements' (1938) "Plant Ecology." Those who are interested in particular fields or problems should look through the past few years of the *Zoological Record* and *Biological Abstracts*. *Bulletin* 39 of the U. S. National Museum gives instructions for collecting and caring for various types of animals. "Culture Methods for Invertebrate Animals" (Galtsoff, Lutz, Welch & Needham 1936) gives general directions for collecting and rearing. Carpenter's (1938) recent "Ecological Glossary" defines terms. Most authors will be willing to send reprints of their papers to those who are attempting to carry on work in the same fields. One who is connected with an educational or scientific institution can of course obtain advice and information from members of the staff. The field covered by ecology is so broad that appeal must be made continually to specialists in others.

New Methods.—Any investigator or teacher should be continually on the alert for new methods that may be taken from other fields and applied to his own. Such inventions as hydrom-

eters, pH indicators, photoelectric cells, and thermocouples have opened new possibilities for the investigation of the problems of biology. New discoveries often result from the development of a new method. Every ecologist should be thinking continually on how his observations may be made more penetrating and more accurate.

CHAPTER XVII

PROBLEMS OF ECOLOGY

Modern Ecologic Investigations.—When an ecologist attempts to study the relations of organisms to environment he is confronted with very intricate problems. Changeful animals which continually vary with their metabolic state, stage in life cycle, and other inherent qualities live in complex and changeful environments where many conditions fluctuate with daily, lunar, and seasonal rhythms and where progressive successional changes may transform a habitat completely. Air that is saturated with water vapor at 10°C. is not so when warmed to 30°C.; water saturated with oxygen at 30°C. will be quite deficient if cooled to 10°C. In such situations an ecologist must have conceit enough to keep on trying to discover new things in spite of continual failures and discouragements and humility enough to recognize that he often discovers only half truths or facts which obtain under the peculiar conditions that he has encountered.

Scope and Character of Problems.—Modern ecology has developed from the "natural history" of the last generation. It includes a clearly defined field—the relations of plants and animals to environment. Plants and animals when present in a particular part of the earth are as much a part of an environment as are soil, water, and air. As in all scientific investigations an ecologist learns facts by observation and experiment. He may go to a particular habitat; record as accurately as possible the numbers of various species that occur; make detailed observations on the condition of various physical factors, such as temperature, light, salinity, soil, currents; and from these facts give a picture of a community and the environment in which it is characteristic. This is observation. On the other hand an ecologist may take a plant or animal into a laboratory where environmental conditions may be controlled and test its ranges of toleration for various factors. This is experimental procedure. Of course some experiments may be conducted in field as well as laboratory. Ecology has many problems that await solution. Some of these

are purely scientific, and others are economic. The best type of research is often done by an ecologist who is not above working on something that has "economic" features but who proceeds in a thoughtful way to investigate all fundamental aspects of his problem. Often facts of great economic importance are discovered by pure scientists who are interested primarily in the increase of knowledge. An ecologist must have knowledge of and interest in the *magnalia naturae*, or the greater problems of biology (Thompson 1912). His problems often make him consider relations to evolution, nature of living things, origins of habitats and organisms, and countless other aspects of the universe as it is today and has been in the past. When possible, investigations should be carried on with living plants and animals in the field; but ecology must take every possible means to go forward. No ecologist can know enough to solve his problems completely. One must therefore often ask aid from physicists, chemists, geologists, geographers, foresters, fishermen, mathematicians, classical scholars, and others who can in any way help to advance knowledge.

SURVEYS

Types of Surveys.—An area of the earth or a particular habitat may be surveyed in various ways. The simplest type of survey is the preparation of a faunal or floral list of animals or plants that occur in a particular place. Such a list may be elaborated with observations on periods of activity and dormancy, migrations, food chains, reproductive periods, life histories, habitat preferences, etc. Some surveys are merely accurate counts by refined methods of numbers of various species present. Those that occur are called dominants, codominants, subdominants, affluents, etc. Some surveys attempt to find the relations of present distribution to that in the past. Surveys may be limited to narrow ranges, as the consortes of a particular plant or animal, the organisms found in the home of an animal, or any other limited habitat. All of these types are of some value (Adams 1913), but any survey should be conducted with as much insight as possible. An ecologist should not be satisfied with a mere list but strive to solve as far as he may all factors that contribute to nature as he finds it. Much of ecology is the determining of where, how, and why animals live.

Relation of Past to Present Distribution.—The present distribution of animals in any region depends on the past. Animals had their past evolution under particular environmental conditions and have gradually developed ranges of toleration which limit them to particular habitats. The tetrapods were probably not forced to become terrestrial on account of progressive aridity but developed when great, stagnant, swampy regions made aquatic habitats deficient in oxygen and thus forced certain vertebrates to breathe air (Case 1926, Pearse 1936). Certain groups of animals have long been quite limited, whereas others range through a variety of habitats. Palaemonid shrimps range through ocean and freshwater, but atyids have long been confined to the latter (Ortmann 1902). When, why, and how have animals developed limitations? What are the particular factors in their systems of activities that prevent them from extending their ranges; or what fortunate variations enable them to occupy new ecological niches?

Counting Organisms.—It is generally true that the more accurate scientific observations are the more valuable they are. The foundations of all science are mathematical. All a scientist can do is determine how many, how much, how fast, how long; his daily tasks are largely counting, weighing, and measuring. Ecologists have attempted to attain accuracy in their study of environments by the use of such devices as quadrats, transects, closing nets, calibrated plankton pumps, insect traps, determinate net catches, soil samplers, and cultures. Thus some knowledge has been gained of the numbers of organisms present in various types of soils (Waksman 1932); populations of plankters; numbers of birds, mammals, and invertebrates present in limited areas. Comparative numerical differences have furnished the basis for designating dominants and naming communities. However, there is still much to be learned concerning the numbers of animals present in habitats. Counting remains an important means.

Habitat Studies.—Certain habitats, such as lakes, pasture lands, and particular regions of the ocean, have been rather thoroughly studied, and their communities and seasonal variations in physical characteristics are well understood. A simple, limited habitat, such as a small artificial reservoir or a barren desert where few species occur, is comparatively easy to study

and understand; but a complex habitat, like a tropical rain forest, is so varied that it is difficult to study completely. There is still much to be done in habitat surveys in all parts of the world. In this connection transition zones between great ecologic realms are of particular interest—shore lines between water and land habitats, timber lines between forested and nonforested areas, etc. Such media as freshwater and ocean are perhaps better known as habitats than are soil and wood. There are two aspects to the study of any habitat: a determination of environmental characteristics; and a study of communities, their fluctuations, cycles, and interrelations. Valuable studies have been made of very limited habitats, such as the population of one species of plant, the insect visitors to a particular type of flower, the inhabitants of rodent burrows and bird nests, and the guests of colonial insects. More such investigations should be made. They give insight into relations of communities and societies.

Species Studies.—Excellent contributions to ecological literature have been made by those who have studied one species in great detail. Such investigations are usually without the superficiality that often attends general habitat surveys. They give opportunity to understand thoroughly anatomy, physiology, life history, cyclic variations, etc. In this connection animals that live in peculiar habitats are of special interest because they give insight into relations to particular ecological factors. Abundant and rare species are also desirable for study because an understanding of their relations to environment may lead to an insight into reasons for success and dominance or the penalties of specialization. There is an opportunity for any young ecologist in any locality. He may look over his local fauna and ask himself why this species is abundant or that one, rare; then proceed to discover how and why.

Classification of Habitats.—The designation of habitats depends on such factors as reaction of soil and salinity of water and on the communities that dwell in and modify them. The basis for proper classification must come through long-continued surveys of physical conditions and populations.

ADAPTATION

Meaning of Adaptation.—There is a clique of modern biologists who resent the use of the word "adaptation" because they feel

that it is teleological. To most ecologists adaptation is a real thing if it is taken to mean that organisms in a general way fit environment, without any necessary implication as to how or why they do fit. The fact that an organism is alive is evidence that it does fit—perhaps more or less ineffectively, but it must fit to such a degree that its metabolic activities and life cycle can continue. One of the problems of ecology is to discover how and why animals are adapted.

Morphological and Physiological Adaptations.—Some plants and animals are so adapted morphologically and physiologically that they are commonly used by ecologists as "indicators" of certain environmental conditions. A jerboa belongs in the desert; insectivorous plants commonly grow on peaty, acid soils. It is the problem of ecologists to discover morphological and physiological bases for fitness. Sometimes the reasons for survival, success, and dominance are quite apparent; at others they are obscure and difficult to determine. Negroes seldom have heavy hookworm infestations, but white men may support thousands of worms and suffer from hookworm disease. The skin of negroes is so thick that few hookworm larvae can penetrate it, but that of white men is thin enough to permit many larvae to bore through it from polluted soil. Why negroes usually have light infestations of yellow fever whereas white men often die from the same cause is not known. This is one of the problems of ecology.

Toleration.—Though animals flourish best under optimum conditions they tolerate a certain range of variation above or below them. Optima and ranges of toleration may be determined experimentally by obtaining data on survival, metabolic rate, development, growth, reproduction, and other biological phenomena. Leibig's Law of the Minimum formulates the principle that the factor in which an animal can stand least variation is usually the factor that limits its survival. For example, a particular species as an adult may range through a variety of habitats but be able to reproduce in a very limited range of conditions. The land hermit crab, *Coenobita clypeatus* (Fig. 49), wanders widely over land areas but must return to the ocean each year to leave its young for a brief development period in sea water. An animal comes into existence with certain hereditary adaptations and ranges of toleration for variations of condi-

tions in environment. It may modify these to some extent during its life but in general is restricted to a comparatively narrow range. Knowledge of toleration ranges may be of value for scientific purposes, the control of pests, or the propagation of beneficial species. A species that changes its range has already begun to evolve into another species.

Rhythms.—A knowledge of rhythmical behavior in organisms and in environment and correlations between the two is essential for ecology. Organisms have periodic cycles of activity which are inherent in their metabolic systems of activities. They are often nicely adjusted to keep pace with daily, lunar, or annual cyclical changes. Periodism has recently been shown to be controlled by such environmental influences as length of day, critical temperatures, definite ranges of salinity, and other factors. More data in this field should be accumulated.

Succession and Dominance.—As the biota in habitats progresses from pioneer communities to climaxes, definite successional changes take place. It is necessary to know for all sorts of situations how certain communities prepare the way for others, what conditions obtain during each stage of succession, how certain species attain dominance, and other facts concerning succession.

Balance.—An adapted organism can maintain itself in a state of dynamic equilibrium with its environment. Studies such as those of Shelford (1914*b*) should be made in all sorts of habitats to ascertain how the behavior of animals keeps them in the most favorable situations for their activities and how they again find appropriate habitats after floods, storms, and other disturbing influences. The behavior of animals in various habitats should be studied in detail.

COMMUNITIES

Communities.—Knowledge of the interdependence among plants and animals in biomes is the keystone of ecology. Every community should be studied with the object of understanding interrelationships. This involves the study of population fluctuations, food chains, propagations, and successions.

Food Chains.—There is a great dearth of knowledge in regard to the character and amount of food eaten by various animals, especially invertebrates. In general, plants constitute the basic

food, which is devoured by vegetarians, and these in turn by carnivores. Such chains are often built on a "pyramid of numbers"; at the bottom are many small vegetarians, and at the top a few large carnivores. In each habitat food relations must be studied. In the past such studies usually have been rather general. More accurate knowledge is needed of character of foods, frequency of feedings, and amounts eaten.

Reproduction.—Often the limiting factor that confines animals strictly to particular habitats is conditions for rearing offspring. Animals that are hardy at most periods in their life cycles may be delicate and easily destroyed when young. An oyster larva cannot endure low temperatures, and most oysters do not spawn below 20°C., but adults readily survive them. On the other hand an unhatched ascaris larva can easily endure freezing temperatures but succumbs to them quickly as an adult. It is not enough to know the ranges of toleration of an animal in one stage of its life cycle, but studies of various ages should be made. This opens up another series of problems.

Populations.—In any region the numbers of animals vary from time to time. In one year a large group of a particular species may be produced and, if conditions for development are favorable, persist as an abundant type for several years. The study of fluctuations in populations is involved and often difficult, but worthy. It is concerned with basic food supplies, conditions for reproduction, relations between predator and prey, climate, parasites, diseases, balances, successions, and other factors.

PRESERVATION OF NATURAL CONDITIONS

Disturbances of Natural Balances.—Human activities have often upset a balanced climax and produced conditions that were unfavorable to man himself. In certain districts of the western United States the destruction of coyotes has allowed rabbits and other rodents to increase to such an extent that they became serious pests. They not only devoured forage plants but nibbled off the tender shoots of coniferous trees and kept them down to the size of low shrubs. The introduction of exotic species, such as English sparrows and starlings in America, rabbits in Australia, and mongoose in Haiti furnish notable examples of injury that resulted from ill-advised tampering with established biomes.

When there is a desire on the part of politicians, businessmen, or farmers to change natural conditions, projects should be studied by biologists to determine what the possible effects of proposed changes may be. The Ecological Society of America has for years maintained an important Committee on the Preservation of Natural Areas.

Lumbering.—The destruction of forests has often produced profound changes in climaxes. The removal of soil cover is conducive to land erosion and of course changes soil. Leaving slash after lumbering makes the starting and spreading of destructive fires easy. With the removal of forests various plants and animals that have been associated with the original stands are also eliminated. All these matters deserve more study.

Dust.—Soil-depleting agriculture, overgrazing, and other destructive processes have often left soil bare so that winds drift sand and silt about and cause great damage to adjacent natural areas and the denuded regions, especially in dry years. In the western United States these matters recently have been the subject of extensive inquiry by scientific men.

Pollution.—Dams, drainage projects, sewage, and industrial waste products often change the character of inclosed marine littoral waters and inland aquatic habitats. Problems associated with the changing of inland waters involve chemical, physiological, and biological studies. Changes produced by modifying the normal succession and climax may favor some few organisms but usually destroy many others. For example, there are a few small animals that flourish in waters heavily contaminated with sewage, but fishes and other types that are desirable from man's point of view are usually absent.

Floods.—Extensive denudation by lumbering, overgrazing, fire, and soil-depleting agriculture removes natural vegetation cover which would normally impede the runoff of water precipitated as rain, snow, or hail. Rivers then overflow, and destructive floods result. The roots, leaves, and stems of plants and the litter that accumulates under them not only cover and protect soil but serve as a veritable sponge which soaks up water rapidly and then slowly releases it to flow through lakes and streams to the oceans of the earth. Flood problems are primarily associated with restoration and maintenance of vegetation cover.

Recreation.—One of the legitimate uses of preserved natural areas is the furnishing of places where men in their leisure time may play or observe plants and animals under natural conditions. In the United States, national forests and parks have contributed much to the everyday life of people. The maintenance of such areas has brought up many problems concerning game management, camping without destroying natural life, regulation of hunting and fishing, restricted grazing, etc. Ecologists have contributed largely to the solution of such problems.

PRODUCTION

Foods.—Food production on land is well under the control of man in pastures and fields. It is made effective through cultivation, the use of fertilizers, pest eradication, and other measures. In freshwater pond culture, fertilizers and nutrients are used somewhat to increase production. In seas most of the food resources depend on natural causes, except for a few instances such as the planting of oysters, mussels, and edible seaweeds in beds. There are many problems that relate to the increase and improvement of foods. To these, geneticists, farmers, biologists, and others must contribute. In the production of foods on natural areas knowledge of such matters as food chains, enemies and parasites of food animals, number and size of animals to be properly taken each season, and critical periods in life histories is essential. In agriculture or aquiculture, methods of cultivating, nourishing, and improving stocks are considered.

Game and Crop Management.—When an area is left more or less in a natural state for the purpose of using its animal life for food or sport, problems of most suitable use, appropriate population density, parasites, protection during critical seasons, natural enemies, diseases, etc., arise. Politicians have secured appropriations and drained swamps that were found to be unsuited for agriculture. Such areas when reconverted into swamp areas may become valuable as resorts for wild fowl and fishes. Practical ecologists attempt to know conditions well enough to be able to judge what types of production are most appropriate for a particular area and how to take care of plants and animals present. A potato grower must select suitable soil, plant, cultivate, and kill phytophagous beetles; a fox raiser worries about suitable food, shelter, exercise, and parasites. Foxes raised in small

fenced areas where soil pollution is easy are often subject to hookworm infestation.

Control of Environment.—Man continually strives not only to continue to exist in his environment but to make it produce more of the things that he desires, so that he may continually live at higher cultural levels. He carefully predicts what weather is to be so that he may most advantageously carry on his activities. He uses various expedients to make more and better organisms grow on available areas. He is ever on the alert to discover new expedients. Scientists, industrialists, and sociologists are all attacking problems in this field. The goal of such investigations is to make environment safer, more comfortable, and more productive. Ecologists must discover how this may be attained.

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